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## THE GENOTYPE CONCEPTION OF HEREDITY<sup>1</sup>

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BIOLOGY has evidently borrowed the terms "heredity" and "inheritance" from every-day language, in which the meaning of these words is the "*transmission*" of money or things, rights or duties—or even ideas and knowledge—from one person to another or to some others: the "heirs" or "inheritors."

The *transmission* of properties—these may be things owned or peculiar qualities—from parents to their children, or from more or less remote ancestors to their descendants, has been regarded as the essential point in the discussion of heredity, in biology as in jurisprudence. Here we have nothing to do with the latter; as to biology, the students of this science have again and again tried to conceive or "explain" the presumed *transmission* of general or peculiar characters and qualities "inherited" from parents or more remote ancestors. The view of natural inheritance as realized by an act of transmission, viz., the transmission of the parent's (or ancestor's) *personal qualities* to the progeny, is the most naïve and oldest conception of heredity. We find it clearly developed by Hippocrates, who suggested that the different parts of the body may produce substances which join in the sexual organs, where reproductive matter is formed.

<sup>1</sup> Address before the American Society of Naturalists, December, 1910.

Darwin's hypothesis of "pangenesis" is in this point very consistent with the Hippocratic view, the *personal* qualities of the parent or the ancestor in question being the heritage.

Also the Lamarckian view as to the heredity of "acquired characters" is in accordance with those old conceptions. The current popular definition of heredity as a certain degree of resemblance between parents and offspring, or, generally speaking, between ancestors and descendants, bears the stamp of the same conceptions, and so do the modern "biometrical" definitions of heredity, *e. g.*, as "the degree of correlation between the abmodality of parent and offspring." In all these cases we meet with the conception that the personal qualities of any individual organism are the true heritable elements or traits!

This may be characterized as the "transmission-conception" of heredity or as the view of *apparent* heredity. Only superficial instruction can be gained by working on this basis. Certainly, medical and biological statisticians have in modern times been able to make elaborate statements of great interest for insurance purposes, for the "eugenics-movement" and so on. But no profound insight into the biological problem of heredity can be gained on this basis, for the transmission-conception of heredity represents exactly the reverse of the real facts, just as the famous Stahlian theory of "phlogiston" was an expression diametrically opposite to the chemical reality. The *personal qualities* of any individual organism do not at all cause the qualities of its offspring; but the qualities of both ancestor and descendant are in quite the same manner determined by the nature of the "sexual substances"—*i. e.*, the gametes—from which they have developed. Personal qualities are then *the reactions of the gametes* joining to form a zygote; but the nature of the gametes is not determined by the personal qualities of the parents or ancestors in question. This is the modern view of heredity.

The main result of all true analytical experiments in questions concerning genetics is the upsetting of the transmission-conception of heredity, and the two different ways of genetic research: pure line breeding as well as hybridization after Mendel's model, have in that respect led to the same point of view, the "*genotype-conception*" as we may call the conception of heredity just now sketched.

Here we can not trace the historical evolution of the ideas concerning heredity, not even in the last ten years, but it must be stated as a fact that a very great number of the terms used by the modern biological writers have been created under the auspices of the transmission-conception, and that perhaps the greater number of botanists and zoologists are not yet emancipated from that old conception. Even convinced Mendelians may occasionally be caught using such words as "transmission" and other now obsolete terms.

The science of genetics is in a transition period, becoming an exact science just as the chemistry in the times of Lavoisier, who made the balance an indispensable implement in chemical research.

The "*genotype-conception*," as I have called the modern view of heredity, differs not only from the old "*transmission-conception*" as above mentioned, but it differs also from the related hypothetical views of Galton, Weismann and others, who with more or less effectiveness tried to expel the transmission-idea, having thus the great merit of breaking the ground for the setting in of more unprejudiced inquiries. Galton, in his admirable little paper of 1875, and Weismann, in his long series of fascinating but dialectic publications, have suggested that the elements responsible for inheritance (the elements of Galton's "*stirp*" or of Weismann's "*Keimplasma*") involve the *different organs* or tissue-groups of the individual developing from the zygote in question. And Weismann has furthermore built up an elaborate hypothesis of heredity, suggesting that discrete particles of

the chromosomes are "bearers" of special organizing functions in the mechanism of ontogenesis, a chromatin-particle in the nucleus of a gamete being in some way the representative of an organ or a group of tissues.

These two ideas: that "elements" in the zygote correspond to *special organs*, and that *discrete particles of the chromosomes* are "bearers" of special parts of the whole inheritance in question are neither corollaries of, nor premises for, the stirp- or genotype-conception. Those special ideas may have some interest as expressions of the searching mind, but they have no support in experience; the first of them is evidently erroneous, the second a purely speculative morphological view of heredity without any suggestive value.

The genotype-conception of the present day, initiated by Galton and Weismann, but now revised as an expression of the insight won by pure line breeding and Mendelism, is in the least possible degree a speculative conception. Of all the Weismannian armory of notions and categories it may use nothing. It is a well-established fact that language is not only our servant, when we wish to express—or even to conceal—our thoughts, but that it may also be our master, overpowering us by means of the notions attached to the current words. This fact is the reason why it is desirable to create a new terminology in all cases where new or revised conceptions are being developed. Old terms are mostly compromised by their application in antiquated or erroneous theories and systems, from which they carry splinters of inadequate ideas, not always harmless to the developing insight.

Therefore I have proposed the terms "gene" and "genotype" and some further terms, as "phenotype" and "biotype," to be used in the science of genetics. The "gene" is nothing but a very applicable little word, easily combined with others, and hence it may be useful as an expression for the "unit-factors," "elements" or "allelomorphs" in the gametes, demonstrated by modern Mendelian researches. A "genotype" is the sum total of



all the "genes" in a gamete or in a zygote. When a monohybrid is formed by cross fertilization, the "genotype" of this  $F_1$ -organism is heterozygotic in one single point and the "genotypes" of the two "genodifferent" gametes in question differ in one single point from each other.<sup>2</sup>

As to the nature of the "genes" it is as yet of no value to propose any hypothesis; but that the notion "gene" covers a reality is evident from Mendelism. The Mendelian workers have the great merit of being prudent in their speculations. In full accordance with this restraint—a quite natural reaction against the morphologico-phantastical speculations of the Weismann school—it may be emphatically recommended to use the adjectival term "genotypical" instead of the noun "genotype." We do not know a "genotype," but we are able to demonstrate "genotypical" differences or accordances. Used in these derivated ways the term "gene" and "genotype" will prejudice nothing. The very appropriate German term "Reaktionsnorm" used by Woltereck is, as may be seen, nearly synonymous with "genotype," in so far as the "Reaktionsnorm" is the sum total of the potentialities of the zygotes in question. That these potentialities are partly separable ("segregating" after hybridization) is adequately expressed by the "genotype" as composed of "genes." The "Reaktionsnorm" emphasizes the diversity and still the unity in the behavior of the individual organism; certainly, the particular organism is a whole, and its multiple varying reactions are determined by its "genotype" interfering with the totality of all incident factors, may it be external or internal. Thence the notion "Reaktionsnorm" is fully compatible with the genotype-conception.

The genotypes can be examined only by the qualities and reactions of the organisms in question. Supposing

<sup>2</sup> They may therefore be characterized as "mono-genodifferent"; this term and the further terms "di-genodifferent" and so on, may or may not be of any use.

that some organisms of identical genotypical constitution are developing under different external conditions, then these differences will produce more or less differences as to the personal qualities of the individual organisms. By simple inspection of series of different individuals it will be quite impossible to decide if they have or have not the same genotypical constitution—even if we know them to be homozygotic.<sup>3</sup> We may easily find out that the organisms in question resemble each other so much that they belong to the same “type” (in the current sense of this word), or we may in other cases state that they present a disparity so considerable that two or more different “types” may be discerned.

All “types” of organisms, distinguishable by direct inspection or only by finer methods of measuring or description, may be characterized as “*phenotypes*.” Certainly phenotypes are *real things*; the appearing (not only apparent) “types” or “sorts” of organisms are again and again the objects for scientific research. All typical phenomena in the organic world are *eo ipso* phenotypical, and the description of the myriads of phenotypes as to forms, structures, sizes, colors and other characters of the living organisms has been the chief aim of natural history, which was ever a science of essentially morphological-descriptive character.

Morphology, supported by the huge collections of the museums, has of course operated with phenotypes in its speculations concerning phylogenetic questions. The idea of *evolution by continuous transitions* from one “type” to another must have imposed itself upon zoologists and botanists, because the varying external conditions of life are often<sup>4</sup> shifting the phenotypes in very fine gradations; but also—and that is an important point—because there may always be found considerable genotypical differences hidden in *apparently homogeneous populations*, exhibiting only one single “type” around

<sup>3</sup> Here we are not concerned with the question of variable dominance, etc.

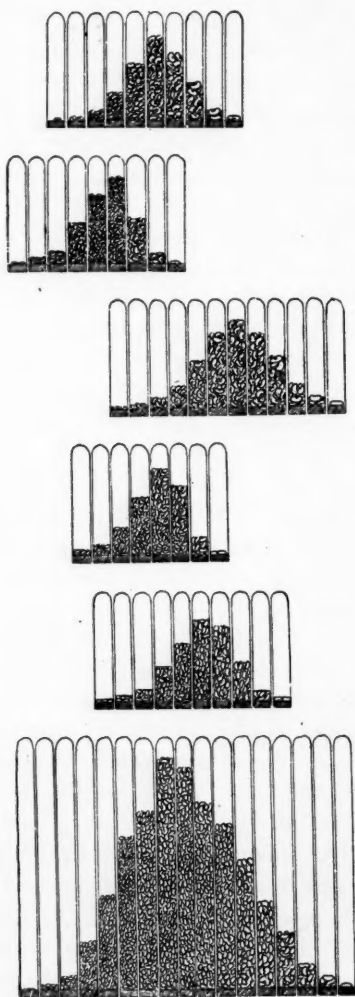
<sup>4</sup> Not always, as Bateson has the merit of having emphasized.

which the individuals fluctuate. For the descriptive-morphological view the manifestations of the phenotypes in different generations are the main point, and here the transmission-conception immediately announces itself. Hence we may adequately define this conception as a "phenotype-conception" in opposition to the genotype-conception.

As already stated, the genotype-conception has been gained in two ways: pure line breeding and hybridization. The first way leads to an analysis of the existing stocks or populations, the second way may realize an analysis of the genotypical constitution of the individuals. The analysis of populations has its most obvious importance in all such cases, where the phenotypes are quantitatively characterized. Even where individuals with considerable genotypical differences co-exist, the population may—by simple inspection or by statistical appreciation—seem to exhibit only one phenotype, this being usually characterized by the average measure of the individuals (dimensions, weight, intensity of any quality, number of organs and so on). This is due to the fluctuating variability swamping all limits between the different special phenotypes in question (see the diagram).

Populations of self-fertilizing organisms (several cereals and beans, peas and others) have offered the starting point for *pure line breeding* as a scientific *method of research*. A pure line may be defined as the descendants from one single homozygotic organism, exclusively propagating by self-fertilization. "Pure line" is a merely *genealogical term*, indicating nothing as to the qualities of the individuals in question. A "line" ceases to be "pure" when hybridization (or even intercrossing) disturbs the continuity of self-fertilization.

From a population of homozygotic self-fertilizers there can be started (isolated) as many pure lines as there are fertile individuals—of course very many of such pure lines will be quite identical in genotypical constitution and might in reality belong to one and the



## EXPLANATION OF DIAGRAMS

DIAGRAMS SHOWING FIVE DIFFERENT PURE LINES OF BEANS AND A "POPULATION" FORMED BY THEIR UNION. In each case the beans enclosed in glass-tubes are marshalled in equidistant classes of length; identical classes are superposed. The pure lines show transgressive fluctuation: it is mostly impossible to state by simple inspection of any individual bean the line to which it belongs.—The fluctuations about the average length (the phenotype) within the pure lines as well as in the mixed population show no characteristic difference.

same pure line if the genealogy was but sure. The guarantee of the descendance is thus a main point in the principle of pure lines. Identity of genotypical nature is not at all a proof for identical genealogy: the widespread confusion of "resemblance" with "genealogical relation" is the root of much evil—of which the statistics of biometricians have given us some instances.

The isolation of pure lines from plant-populations has been the instrument for gaining the conviction that *selection is not able to shift the nature of genotypes*. The well-known displacement of the "type" of a population by selection—this displacement proceeding from generation to generation in the direction indicated by the selection—is due to the existence *a priori* of genotypical differences in such populations (see the diagram). By selection a relatively great number of those organisms, whose genotypical constitution is favorable for the realization of the desired degrees of any character, will be saved for reproduction; hence the result of the selection!

Within pure lines—if no mutation or other disturbances have been at work—or within a population in which there is no genotypical difference as to the character in question, selection will have no hereditary influence. This result has in recent years also been reached by several other experimenters in genetics. Here I also may recall the brilliant experiments of H. S. Jennings with *Paramecium*, experiments which have been carried out quite independently of my own researches and which have been of great importance for the propagation and support of the genotype-conception. The bearing

It can not be detected by inspection that the five upper diagrams represent phenotypes which are genotypically homogeneous, while the nethermost diagram—the sum of the others—indicates a phenotype masking five others. That these five phenotypes all are genotypically different is known *a priori* in this special case, but it could not be discerned by simple inspection.—In the population genotypical differences are combined with merely individual fluctuations; within the single pure line only such fluctuations are seen. Hence, while selection within a *pure line* will have no hereditary influence, it is evident that any selection in the *population* must shift or move the "type" of the progeny in the direction of selection.

of these experiments has been attacked on the ground that the *Paramœciums* multiply asexually; but this matter seems to me of no importance in the present case. The experience that pure-line breeding of plants and pure-strain cultures of micro-organisms, in full agreement, demonstrate the non-adequacy of selection as a genotype-shifting factor, is a circumstance of the greatest interest. Also Woltereck's experiments with *Daphnias*, the important researches of Wolff, and the highly interesting indications of C. O. Jensen as to bacteria may be mentioned here as further supports for this view. Quite recently Pearl has arrived at the same conclusion as to the egg-production by fowls.

The famous Galtonian law of regression and its corollaries elaborated by Pearson pretended to have established the laws of "ancestral influences" in mathematical terms. Now, by the pure-line explanation of the well known action of selection in poly-genotypic populations, these laws of correlation have been put in their right place; such interesting products of mathematical genius may be social statistics *in optima forma*, but they have nothing at all to do with genetics or general biology! Their premises are inadequate for insight into the nature of heredity.

Ancestral influence! As to heredity, it is a mystical expression for a fiction. The ancestral influences are the "ghosts" in genetics, but generally the belief in ghosts is still powerful. In pure lines no influence of the special ancestry can be traced; all series of progeny keep the genotype unchanged through long generations. A. D. Darbishire's laborious investigations as to the classical object of Mendel's researches, green and yellow peas, may even convince a biometrician that the ancestral influence is zero in "alternative inheritance." Ancestral influence in heredity is, plainly speaking, a term of the "transmission-conception" and nothing else. The characters of ancestors as well as of descendants are both in quite the same manner reactions of the geno-



typical constitution of the gametes in question. Particular resemblances between an ancestor and one or more of his descendants depend—so far as heredity is responsible—on corresponding particular identities in the genotypical constitution, and, as we have urged here, perhaps to excess, the genotype is not a function of the personal character of any ancestor.

The genotypic constitution of a gamete or a zygote may be parallelized with a complicated chemico-physical structure. This reacts exclusively *in consequence of its realized state*, but not in consequence of the history of its creation. So it may be with the genotypical constitution of gametes and zygotes: its history is without influence upon its reactions, which are determined exclusively by its actual nature.

The genotype-conception is thus an "ahistoric" view of the reactions of living beings—of course only as far as true heredity is concerned. This view is an analog to the chemical view, as already pointed out; chemical compounds have no compromising ante-act,  $H_2O$  is always  $H_2O$ , and reacts always in the same manner, whatsoever may be the "history" of its formation or the earlier states of its elements. I suggest that it is useful to emphasize this "radical" ahistoric genotype-conception of heredity in its strict antagonism to the transmission- or phenotype-view.

As to the evolution of human civilization we meet with *true ancestral influences*, viz., the *tradition* (comprising literature, monuments of art, etc., and all forms of teaching). Tradition is playing a very great rôle, but tradition is quite different from heredity. Nevertheless there may often be danger of confusion, and here the use of false analogs is not harmless. So an obscure metaphor is involved in archeologists' reference to Greek temples as "ancestors" of some types of Christian churches, or in their speaking of the descent of violins from more primitive "ancestors." Certainly, evolution of types of tools, instruments and implements of all kinds is—at least partially—going on by means of select-

ive factors combined with tradition, the latter not only conserving the valuable types but actively stimulating their improvement. But all this has nothing at all to do with the biological notion of heredity. It is of course interesting to see that the idea of "evolution by selection" has won credit in archeology, sociology, etc., but this involves nothing as to genetics, for which "tradition" is irrelevant.

The very "radical" form of the genotype-conception advocated here may be too "theoretical" to be carried through in all its consequences in cases of practical experiments in genetics. In nature and even in the chemical factories the chemical compounds are not always to be had in quite pure state. The history of a preparation may sometimes be traced by accompanying impurities. As to the analogy with the genotypes we touch here the question whether the genotypical constitution of a gamete may not be accompanied by some accessorial or accidental "impurities" from the individual organism in which the gamete was developed.

Here we meet with the cases of "spurious" heredity, *e. g.*, the infections of the gametes or zygotes as may be seen in certain cases of tuberculosis, syphilis, etc. Such and other forms of spurious heredity may have the appearance of "hereditary transmission" or "ancestral influence"; but theoretically they do not interfere at all with the genotype-conception of heredity. In such interesting cases as that detected by Correns, *viz.*, the "heredity" of a special form of albinism by "transmission" through the plasm of the ovum—the sperm not transmitting this character—we may at the first glance be puzzled. Nevertheless, as Correns himself points out, here we have certainly to do with a pathological state of the plasm or the chromatophores in question, and that may perhaps be the reason for the lack of heredity through the sperm which carries no (?) plasm or only a small quantity. The etiology of such abnormalities being as yet quite unknown, it may often be very difficult to distinguish them clearly from "genotypically" de-

terminated abnormalities which show the normal form of heredity through both ovum and sperm. The case quoted demands further experience and seems not to be in accord with results of Baur's experiments. At any rate, there may be several difficulties to overcome in the full and consistent application of the genotype-conception, difficulties that may be characterized as perturbations by infection or contamination. And hereby it must be remembered that theoretically, as well as practically, there are no sharp limits between "normal" and "pathological" manifestations of life. "Nature is beautiful, but not correct," is a Danish saying.

The principle of pure lines or, generally, pure culture, is of importance also for elucidating the celebrated question of the inheritance of "acquired characters." Mendelism and pure-line researches are here in the most beautiful accordance, both emphasizing the stability of genotypical constitution; the former operating with the *constituent unities*, the latter with the behavior of the *totality* of the genotypes in question. The brilliant work of Tower with *Leptinotarsa* and the highly suggestive injection experiments of MacDougal indicate that changes of the genotypical constitution are produced by steps, discontinuously. And as yet no experiment with genotypically homogeneous cultures has given any evidence for the Lamarckian view, the most extreme "transmission"-conception ever issued. As to bacteria, the important experiments recently made by C. O. Jensen for the purpose of changing their types through adaptation have given not only absolutely negative results, but have demonstrated the fallacy of some positive indications by previous authors. Lamarckism and selectionism are certainly at bottom the same thing: the belief in personal qualities being "transmitted" to the offspring. Observations in impure populations are now their places of resort; nevertheless, it is granted that their history in biology as suggestive ideas has been most glorious.

Apropos, some cases of apparent action of selection

may have direct touch with Lamarckian ideas, as, *e. g.*, De Vries's selection of buttercups, recently quoted by Jennings as "the only case that he has found" indicating hereditary action of selection: "Here, after selection the extreme was moved far beyond that before selection." And Jennings says: "Possibly repetition with thorough analytical experimentation will show that something besides selection has brought about the great change. But at present the case stands sharply against the generalizations from the pure line work."

Certainly Jennings is in reason, when he, on the ground of his own masterly researches, looks out for "something besides selection." There are three directions for the inquiry here. First, the strong evidence that the buttercup-population was not at all homogeneous. Secondly, the possibility of intercrossing. I only need to point out the beautiful researches of Shull as to the effect of intercrossing in maize. The heterozygotes were here larger and more productive than the pure strains. The surprises of heterozygotic "constructions" or of new combinations in  $F_2$  may perhaps be responsible for the case of De Vries's buttercups; I shall not try to discuss it. But, thirdly, we have an instance pointed out several times by De Vries himself, viz., the *combination of selection with nourishment*: "*la sélection c'est l'alimentation*" as it has been said. I suppose that we have here the essential point. The buttercups in culture have been better nourished than before the experiments. Hence, the "best" genotypes having been selected from the population and submitted to "better" nourishment, the result would easily be a moving of the extremes far beyond those before selection. The buttercup-case seems to me to present no difficulties for the genotype-conception.

The practical breeders are a somewhat difficult people to discuss with. Their methods of selection combined with special training and "nurture" in the widest sense of this word are mostly unable to throw any light upon questions of genetics, and yet they only too frequently

make hypotheses as to the nature of heredity and variability. Darwin has somewhat exaggerated the scientific value of breeders' testimonies, as if a breeder *eo ipso* must be an expert in heredity. As to the principle of pure lines it has been occasionally vindicated by German authors, *e. g.*, K. v. Rümker, that pure line breeding is a thing old and well known. This is quite true; nearly sixty years ago L. Vilmorin not only emphasized in a lucid manner the importance of pure breeding, but he even tried a little to use his experiences theoretically. But it can not be denied that the principle of pure lines, as a true scientific analytical implement, as an indispensable *method of research in heredity*—not merely as a questionable and, at any rate, unilateral and insufficient method of practical breeding—is a novelty from recent years. Had this analytical principle been used in the times of Darwin, or had it even been appreciated in due time by the biometric school, certainly the real bearing of selection might long since have been rightly understood also by the practical breeders of pure strains.

The genotypes may then be characterized as something fixed and may be, to a certain degree, parallelized with the most complicated molecules of organic chemistry consisting of "nuclei" with a multitude of "side-chains." Continuing for a moment such a metaphor, we may even suggest that the genes may be looked upon as analogs of the "radicals" or "side-chains." All such ideas may as yet be premature; but they are highly favored by the recent researches of Miss Wheldale.

> The fixity of a genotypical constitution in question is the conception arrived at by Mendelian and pure line work. Hence there is a *discontinuity* between different *genotypes*. This discontinuity has been energetically contested by several biologists, among whom Woltereck may be pointed out as an important representative. In his very interesting report on experiments with *Daphnias*, Woltereck indicates, as said above, that *selection was as yet ineffective*; moreover he describes a case of *discontinuous alteration* of type (mutation), and his ex-

periments designed to confirm the Lamarckian view have given as yet negative results, even though these may be called "promising," as he says. So all the evidence of his breeding experiments is in reality quite in favor of our genotype-conception!

But how much depends upon our mental eyesight, what we see. Woltereck confesses openly his belief in continuous evolution and remarks that for a convinced selectionist of the Weismann school the new genotype-conception is a "hard blow." The aim of his paper in question is to parry off such blows. Of course this parry can not use his own statements just mentioned; as to their obvious but inconvenient accordance with our conception Woltereck might apply the famous words from Harvey's times: "*video sed non credo*." Hence the arguments must be taken from other observations, and some very instructive results of cultures under varying conditions have supplied the *pièce de résistance* for the discussion. Woltereck is within his right when asserting that we consider different genotypes as having *constant differences* (like different formulas in chemistry). This is an essential point; but Woltereck, admitting no constancy in the differences, tries to demonstrate that our view must be fallacious.

In a very suggestive manner he presents "phenotype-curves" for several pure strains. These curves are graphical schemes expressing (for the strain in question) the average degree or intensity of any particular character as it manifests itself under different conditions, *e. g.*, the relative length of heads by poor, intermediate and rich feeding, etc. Such "phenotype-curves" may indeed be very useful as records of the behavior of the organisms in question, and they mark certainly a valuable progress in descriptive methods.

The phenotype-curves of the *Daphnias* in question sometimes show rather constant differences between the pure strains compared; but mostly this is not the case. Especially under extreme conditions, *e. g.*, with poor or even with very rich feeding, some of the curves are con-



fluent. So the differences between the phenotype-curves may vary considerably or may even vanish entirely. These experiences agree with numerous observations of Wesenberg Lund as to the *Daphnias* in the Danish lakes, and there is no doubt as to their correctness.

But when Woltreck thinks that these facts are inconsistent with the existence of constant differences between the genotypes, he shows himself to have totally misunderstood the question! Of course the *phenotypes* of the special characters, *i. e.*, the *reactions of the genotypical constituents*, may under different conditions exhibit all possible forms of transition or transgression—this has nothing at all to do with constancy or inconstancy of genotypical differences.

Every student of genetics ought to know this; some few examples may suffice to enforce it: Temperature has great influence upon the intensity of color in flowers; all shades of intensity from saturated reddish-blue to pure white may be observed with different temperatures in lilac flowers of the "colored" varieties. Such pure white flowering individuals are—as to color—phenotypically not distinguishable from genotypically pure "white" varieties. Nobody will assume that there should be *genotypical* transitions here! Pure lines of beans may in one year be different in size, *e. g.*, the average of the line *A* exceeding that of *B*. In another year *B* may exceed *A*, or their average sizes may be practically identical. Differences of soil may produce something similar, and it is well known to breeders that some strains of wheat yield relatively much better than others on rich soil, while the reverse is realized on poorer soils. In four subsequent years two pure lines of barley, both characterized by a considerable degree of disposition to produce vacant spikelets (aborted grains) in the heads, presented the phenotypes here indicated in percentages of such vacancies.

Pure line <i>L</i> :	30	33	27	29
Pure line <i>G</i> :	5	45	3	28

The genotype-differences are nevertheless constant; the "Reaktionsnorms" of the organisms in Woltereck's cases, as well as in the examples just cited, are of course *eo ipso* "constantly different" just as well as the "Reaktionsnorms" of different chemical compounds. And as to chemical analogies it may perhaps be useful to state that different chemical compounds (the structural or constitutional differences of which surely are granted to be discontinuous and constant) may sometimes show "reaction-curves" highly resembling Woltereck's "phenotype-curves." It is, I suppose, quite sufficient to point out the temperature-curves of solubility for different salts of sodium and other metals. These curves interfere in different ways, cutting each other or partially confluent, in analogy with Woltereck's phenotype-curves.

The essential point in the whole matter is, of course, that a special genotypical constitution always reacts in the same manner under identical conditions—as all chemical or physical structures must do. Differences in genotypical constitution (as well as differences in chemical or physical nature) are not bound to manifest themselves at all—and still less to do so in the same sense—under all conditions. Sometimes even quite special conditions may be required for the realization of possibilities ("Potenzen," as some German authors are saying), due to a special genotypical nature: This is a well-known fact in physiology as in the fine art of gardening. Baur has long since emphasized the importance of this point for the Mendelian researches.

So the criticisms of Woltereck as to the genotypical discontinuity and constancy are only based upon a regrettable misconception of the genotype-notion. Over and over we find in current literature this confusion of genotypes with phenotypes, and we even have met with the idea, that the *Daphnias* of a lake may in summer diverge in different races or varieties, but that in winter they converge into one single race! In this statement of Wesenberg Lund, the author regards of course only the phenotypes in a purely descriptive manner. It is evident

that Woltreck's view has been influenced by Wesenberg Lund in this matter; but what might be fairly excused in the latter is not allowable for an experimenter pretending to work with cardinal questions of genetics.

Discontinuity and constant differences between the "genes" are the quotidian bread of Mendelism, and here the harmony of Mendelism and pure line work is perfect. We have dealt with some recent criticism of the pure line results; now it is time to look at Mendelism. The astonishing evolution of this mode of research has given an almost interminable stock of special results, and cases that at first might seem incompatible with the Mendelian views have been analyzed more thoroughly on a large scale and have shown themselves quite in accordance with Mendelism. The magnificent book of Bateson gives a full account of this prosperous state of Mendelian research. And it may be evident that Mendelism gives the most striking verification of the essential point in Galton's "stirp-hypothesis": the inadequacy of the personal quality in heredity. At the same time it overthrows totally the idea of "*organs*" as being represented by the unities of the "stirp," pointing out that the personal qualities of *the organism in toto* are the results of the reactions of the genotypical constitution. The segregation of one sort of "gene" may have influence upon the whole organization. Hence the talk of "genes for any particular character" ought to be omitted, even in cases where no danger of confusion seems to exist. So, as to the classical cases of peas, it is not correct to speak of the gene—or genes—for "yellow" in the cotyledons or for their "wrinkles,"—yellow color and wrinkled shape being only reactions of factors that may have many other effects in the pea-plants. It should be a principle of Mendelian workers to minimize the number of different genes as much as possible.

Here we meet with the questions of correlation and "coupling" of genes. I can not here enter into a discussion as to the notion of "correlation" with its several meanings; in my "*Elemente der exakten Erbliehkeits-*

lehre" a rather full discussion is to be found. I may only point out here that many cases of presumed correlation may simply be cases of two or more characters (reactions) due to the presence—or even absence—of one single gene. The phenotypically distinct and even diversely localized "characters" convey easily the impression that they are reactions of different genes.

The highly interesting experiences of Correns, Doncaster, Morgan, Spillman and others as to the sex-determining factors, are in some way connected with researches of correlation and "coupling" of genes. The discussion of the ingenious Bateson-Punnett scheme for *Abraxas* and Morgan's suggestive schemes as to *Drosophila* may favor the idea of what may be called "ramified" genes. Castle has in his splendid researches as to color-factors in rabbits, etc., initiated a systematic description of the (partially) analyzed genotypes, somewhat resembling the formulas of organic "structural chemistry." If we suggest an analogy between the radicals of chemistry and the genes, the (partial) genotype-formulas in Castle's manner may be able to demonstrate ramifications of the genes inserted upon the main group of the genotype-constituents. Pausing a moment on this metaphor, it may be suggested that the "branch," or "branches" of a ramified gene may be more difficult to separate from its "trunk" than the whole gene from the totality of the genotype. I shall here only ask if such views may be of any use as working hypotheses. Their bearing as to the realization of mutations is obvious,—but the purely speculative nature of these suggestions can not as yet warrant a longer discussion here.

It should always be borne in mind that the Mendelian analysis is *purely relative*. Baur and Shull and even several others have emphasized this fact when discussing the segregations in their experiments, and Shull has clearly pointed out that it may be quite impossible to indicate whether a particular reaction (character) is due to something positive or to the lack of a factor in the genotypical constitution. All that can as yet be deter-

mined in this regard by Mendelian analysis is the *number of differing points* between the two gametes forming a heterozygote. Such differences may be termed "*geno-differences*." The well-known facts, that a "character" may be dominant in some hybrids but recessive in others, and that segregation in different cases may be very different, indicate that "characters" are complicated reactions. The famous case of Bateson's fowl-hybrids as to the form of comb may here be quoted as an example: In Walnut comb  $\times$  Rose comb the latter is recessive, in Single comb  $\times$  Rose comb it is dominant, and in both cases the segregation gives three dominants: one recessive. Now Bateson has shown that "Walnut" is a compound of Rose- and Pea-comb. Homozygotic Walnut differs from homozygotic Rose only in one point, as does Rose compared with Single. But Walnut-gametes differ from Single-gametes in two points; hence Walnut  $\times$  Single, with Walnut as dominant, segregates in Walnut, Rose, Pea and Single in the proportions 9:3:3:1. Even with this analysis it is as yet not possible to decide whether Single or Walnut is the form of comb for the realization of which the greater number of *positive* factors are required. Suggesting—what seems to be the most probable assumption—that Walnut is the most geno-complicated case, Single may even be an expression for a multitude of genes in the fowl-constitution. The relativity of the analysis by segregation must in all such cases be remembered, and it is quite erroneous to think that dominance indicates the positivity of the "unit-factor" in question: So "Horns" are in Wood's cases dominant in male sheep but recessive in female sheep. And as to analogs with chemical reactions it must be kept in mind that a characteristic reaction may be the consequence of *lack* of any substance as well as dependent upon the *presence* of any special compound in the solution in question.

The elaborate work of Mendelians of recent years has shown very complicated segregations, and the most specialized segregation is almost the most specialized analy-

sis still known of any "character" in question. The "units" or "unit-factors" stated in Mendelian work are consequently quite provisory, depending essentially upon the number of *genodifferences* in the special crossing. Probably it may be discovered that several such "unit-factors" for one character may also be elements for the realization of quite other characters. If this be the truth, then the present state of Mendelism, characterized by the rapidly augmenting number of new "unit-factors" demonstrated in the organization of different biotypes able to hybridize, may be replaced by a period in which many such unit-factors will be identified. At any rate there is no reason to believe that the further Mendelian analysis will augment the number of genes into absurdity. The enormously increasing possibilities of combinations by augmentation of the number of segregable genes are a source of interest also in this connection.

As to cases of hybridization, in which segregation and combination do not suit the Mendelian "laws," it must at first be stated that some apparent exceptions are probably caused by non-homogeneity of the initial material for experiments. The experiments of Correns, Castle, Miss Saunders, Tschermak and others have shown to excess that phenotypes may seem totally "pure" and nevertheless be heterogeneous (*e. g.*, white flowering stocks or albino mice). Thus constancy as to the phenotype of the progeny is no sure proof for genotypical purity or unity. In discussing alternative inheritance we meet with difficulties of the same nature as in regarding fluctuating variability: the inadequacy of phenotype-description as the starting-point for genetic inquiries.

— Secondly, the more or less high vitality of the different combinations of genes in  $F_2$  may perturb the Mendelian results, as Baur has illustrated; in other cases the different degree of facility with which the union of special gametes is realized may influence the relative numbers of representatives in the  $F_2$ -generation, as Correns has demonstrated.



Here we can not discuss the difficulties in a complete carrying through of the Mendelian analysis; Bateson's recent book contains a richness of instances concerning this matter. Only one instance of special importance may be mentioned here, viz., the so-called "*blended inheritance*" opposed to Mendelian segregation or "alternative inheritance." In cases of blended inheritance the genes in question might be supposed to "fuse together" by the act of hybridization, or, in accordance with the presence- and absence-view, the gene unilaterally carried to the zygote might here in some manner be "diluted." In this way, which certainly is very badly compatible with the conception of genes as unit-factors, *failing segregation* might be explained.

Cases of failing segregation seemed to be abundant in the beginning of the modern Mendelian era; Mendel himself pointed out some typical cases in the species-hybrids of *Hieracium*. And Correns's indication as to the constant intermediate stature of maize stems seemed to be a crucial case. Now the insight won by breeding experiments as well as by cytological researches concerning the phenomena of *apogamy* has put the question in a new light. The discoveries of Murbeck, Raunkjær, Ostenfeld, Rosenberg and others have led to quite other explanations as to the constancy of several intermediate hybrid forms. In such cases no segregation is realized, because no gametogenesis is going on—and in such cases there is no reason for supposing any "fusing" or "dilution" of genes. And as to Correns's experiments, this careful author has himself withdrawn the suggestion in question.

But still cases of "blending inheritance" remain. Among these Castle's experiences as to the dimensions of rabbits, especially the length of ears, are the most important and most discussed instances. Castle has in a convincing and suggestive manner demonstrated that the complicated color-characters in rabbits agree with the Mendelian laws. Therefore much stress might be laid upon his indication of cases contrary to these laws.

Crossing short-eared and long-eared races, he gained an  $F_1$ -generation with almost intermediate ears, and here no segregation was observed in  $F_2$ .

But even this case may agree with Mendelian laws. The idea for such interpreting is won—as Lang has clearly pointed out—by means of Nilsson-Ehle's (and East's) experiments, the former concerning the colors of wheat-grains, the latter dealing with the number of "rows" in the ears of maize. Nilsson-Ehle demonstrated that blending of red and white color in wheat is apparently a fiction: The red color is determined by several different genes, acting in the same sense and augmenting the effect of each other. Hence by segregation and new combinations of these approximately equipotent genes a whole series of gradations in red color will be realized. And these gradations must group themselves symmetrically around the phenotype of the  $F_1$  in question. If we have to consider say three genes, A, B and C, we shall for  $F_1$  use the formula AaBbCc, indicating the value 3 which is intermediate between aabbcc as zero and AABbcc as 6. Even in case of no fluctuation such a series must present itself as an almost continuous gradation, and it is not difficult to find out that the progeny of every "class" here will breed true, *i. e.*, the average of the progeny's character will be like the "class" of the parent.

Just so it is in the case of East's experiments with maize, as East himself has clearly illustrated. Thus, well-analyzed instances of heredity in plants, concerning both color-factors and meristic factors may be compared with Castle's case in question. Lang in his interesting criticisms points out that certain irregularities in Castle's  $F_2$ -material give strong evidence for the view that we have no blended inheritance but true segregation here as well as in the cases of Nilsson-Ehle (and, as we may add, in the cases of East). Further analysis may then probably demonstrate in a more direct manner the true nature of the apparent blending in Castle's case; as yet we can

only say that this case does not seem incompatible with Mendelian views. It must also be borne in mind that certainly there have been very *many genodifferences* between the differing races intercrossed in Castle's experiments. Hence these experiments are really operating with highly poly-heterozygotic  $F_1$ -generations. And how great influence upon dimensions (of ears and other parts of the body) those color-determining genes may have exercised can not be easily determined.

As to beans, it is proved that genes, effective in color-reactions, may also have great influence upon the dimensions and forms. So in my crosses a special factor, which makes yellow color turn into brown and causes violet to be turned into black, has a very marked influence upon the size and form of the beans in question. Here exact data are not necessary; the instance exemplifies the two incident matters of fact, viz., that apparently simple "dimensional" or meristic characters may be determined by *several different genes*, and that one sort of gene may have influence upon *several different reactions*.

Then it seems that Mendelian analysis is proceeding in a very prosperous way; but there may be even very narrow limits for this analysis: the entire organization may never be "segregated" into genes! But still there is much to do in carrying through the genotype-conception as far as possible.

As to cytological researches the genotype-conception is as yet rather indifferent. Certainly the process of segregation must be a *cell-action* intimately connected with division. But all the innumerable detailed results of the refined cytological methods of to-day do not elucidate anything as to segregation. It seems to the unprejudiced observer that the much-discussed cytological phenomena of karyokinesis, synapsis, reduction and so on may be regarded rather as consequences or manifestations of the divisions, repartitions and segregations of genotypical constituents (and all other things in the cell) than as their causes. This view is applicable even in those cases

where sex-determination can be diagnosticated cytologically.

In the discussion as to the existence of true *graft-hybrids* the cytological configurations have of course a high importance as *precisely defined characters* of cells in such cases where the cytological elements of the two species in question are different. And, as it may be well known, cytological evidence is not at all favorable for the idea of graft-hybrids. But the use of cytological configurations for diagnosis is quite different from the idea that special cytological elements might have importance for the phenomena of heredity.

The question of *chromosomes* as the presumed "bearers of hereditary qualities" seems to be an idle one. I am not able to see any reason for localizing "the factors of heredity" (*i. e.*, the genotypical constitution) in the nuclei. The organism is in its totality penetrated and stamped by its genotype-constitution. All living parts of the individual are potentially equivalent as to genotype-constitution. In botany there has been no doubt as to this conception, and as to animals, O. Hertwig has for a long time advocated the same view against the views of Weismann and others, who have suggested that ontogenesis is partly determined or at any rate accompanied by a progressive simplification of the "anlagen" (as we say the "genotype-constitution") in the cells of the growing embryo. The agencies of normally varying ambient conditions and the interactions of specialized parts in the developing individual may exercise their strong influence upon the whole phenotypical state of the resulting particular individual. But these factors will as a rule not change or shift the fundamental genotypical constitution of the biotype in question. Later on we shall touch the problem of such genotypical changes (the mutations) induced by external factors.

Here we have to point out the fact that "living matter"—or, with a more precise definition, those substances or structures the reactions of which we call

"manifestations of life,"—is *inter alia* characterized by the property of *autocatalysis*. The autocatalysis of living beings must embrace the totality of their genotypical constituents. It seems to me that this autocatalysis as well as the *compensative and complementary maintenance of genotypical equilibrium* in the organisms, present some of the greatest enigmas of organic life.

The discussion of cytological problems leads us to the question of *pure or impure segregation*. In the beginning of modern Mendelian researches several instances of presumed impure segregation of genes in gametogenesis were discussed, *e. g.*, as to color factors in animals. But more thorough analytical experiments have in many such cases demonstrated "purity" in the gametes, the characters in question having proved to be more complicated reactions than at first supposed. Recently Morgan has discussed the question in a quite new manner, suggesting—as a working hypothesis—that the segregation might be not of qualitative but of merely quantitative nature. Hence the gametes should as a rule not be pure. Nevertheless, as the author illustrates by means of interesting diagrams, the  $F_2$ -generation of a monohybrid with normal dominance might be composed of two classes of individuals sharply defined. And the author suggests that this idea might be able to explain "the graded series of forms so often met with in experience and so often ignored or roughly classified by Mendelian workers."

Here we again touch the question of "blended inheritance." I suppose that the above-mentioned explanations by Lang and East are more consistent with the real nature of the graded series in question. Now the Mendelian work has not only been able to demonstrate that several cases of segregation apparently impure are pure segregations of complicated nature; but even the "spotted conditions" as to color in animals and plants, emphasized by Morgan as a puzzling case, does not seem to present any real difficulty for Mendelian explanation. Certainly such cases as Shull has pointed out, viz., hetero-

zygotic nature being necessary for "mottling" in some special bean-hybrids, may at first glance favor the idea of "spotted conditions" being due to irregular segregation or to different repartition of color-determining factors in the tissues in question. But a closer examination seems to vindicate the real existence of special "spotting factors." The very interesting researches of Lock as to the "Inheritance of certain invisible characters in peas" have clearly pointed out a "spotting" factor or a "pattern"-determiner in peas, independent of any color-manifestation. It must be borne in mind that a multitude of characteristic epidermal "patterns" are found in animals and plants, these patterns concerning all epidermal manifestations and often showing a widely fluctuating variability. As to the realization of all such spots it might be suggested that in neighboring parts of the developing epidermal tissue some little difference of ambient conditions may inhibit or even release reactions, the alternation of which produces the spots.

The whole case seems to be somewhat analogous to the *merely phenotypical phenomena of alternative variability* first pointed out by De Vries, *e. g.*, the alternation of decussated and contorted stems of *Dipsacus*. Here we touch the highly suggestive idea of "*sensible periods*" in ontogenesis or histogenesis emphasized with so good experimental arguments by De Vries. Of course there must be a genotypical fundament for the existence of the alternating character in question, *e. g.*, for the particular nature of the surface of the spots (or for the contortion in *Dipsacus*, etc.); strains without such genotypical fundament will not be spotted (nor produce contorted individuals at all).—These remarks are made only to point out that Morgan may have exaggerated a little his criticisms as to "spotting factors," but I confess that this question is in need of closer analysis.

Then the problem of pure or impure segregation may still be open; but the tendency in modern genetics goes certainly in the direction of establishing pure segrega-



tion as the normal case. If we accept the suggestion of autocatalysis as an essential factor for the propagation of living matter in general, and hence *eo ipso*, for the growth or multiplication of genotypical constituents, we might in case of impure segregation expect frequently to find "dominants" in the progeny of "recessives"; and the numerical proportions of the dominants and recessives in consecutive generations must be rather irregular. But this is not the case. The recent experiments of Darbishire quoted above demonstrate in a beautiful manner the purity of segregation during subsequent generations in Mendel's classical object, the pea.

Francis Bacon says: "Human understanding easily supposes a greater degree of order and equality in things than it really finds." So we may in modern genetics be aware of the relativity and narrowness of our provisorial explanations, remembering Bacon's warning that "many things in nature may be *sui generis* and irregular!" Among the irregularities in heredity we may reckon the mutations, observed in nature as well as in more precisely defined conditions of artificial experiments. From the famous observations of De Vries and the indications of several earlier authors, to the modern experimental researches of MacDougal, Standfuss, Tower, Blaringhem and others, all evidences as to mutations point out the *discontinuity* of the changes in question. Here we need not enter the question; it is sufficient to state that the essential point is the *alteration, loss or gain of constituents of the genotype*. The splendid experiments of Tower as to *Leptinotarsa* have in the most evident manner shown that the factors which produce the mutations in this case, viz., the temperature and state of moisture, are able to act in a direct manner upon the genotypical constitution of the gametes; and Tower has noted the occurrence of Mendelian segregation in hybridizing his mutants with the original unaltered biotypes. There may in some cases be certain puzzling irregularities to be explained by future researches, but it is evident that in all such muta-

tions, discontinuity is the characteristic feature in the change of type.

As to populations, the biotypes of which may practically exhibit continuous transitions—like the case of my own populations of beans—the idea might be born that biotypes are evolved from each other by extremely small steps in genotypical change. Hence such mutations must be practically identical with “continuous” evolution. But there is no evidence for this view. Certainly in such populations the “static” transitions between the genotypical differences manifesting themselves in several characters may be called continuous—but such a “continuity of museums,” as it might be called, is not at all identical with *genetic* continuity. Galton himself has emphasized the capital difference between the notions of continuity in *collections* and continuity in *origin*, and as yet the mutations really observed in nature have all shown themselves as considerable, discontinuous saltations. So in my own still unpublished experiments with pure lines. *Natura facit saltus*. The chemical analog to such mutations may be the formation of homologous alcohols, acids and so on. The greater mutations may be symbolized by more complicated molecular alterations. But such analogs are of very little value for the understanding of genetic evolution.

The genotype-conception supported by the great stock of experiments as to pure line work, Mendelism and mutations does not consider *personal adaptation* as a factor of any genetic importance. Phrases as “characters, won by adaptation and having successively been hereditarily fixed,” are without meaning from our point of view. Hence much talk of adaptive characters successively gained seems to us an idle matter. A closer study of desert-organisms and the like may elucidate such things; here the suggestive researches of Lloyd as to stomates in desert plants may be pointed out. And as to the old question of “mimicry,” this problem in the famous cases of butterflies has in a most convincing manner been put

into Mendelian terms by the observations and experiments of Punnett, de Meijere and others. This stronghold of the united Lamarckism and selectionism has now been conquered for Mendelism, *i. e.*, for the genotype-conception.

The genotype-conception here advocated does not pretend to give a true or full "explanation" of heredity, but may be regarded only as an implement for further critical research, an implement that in its turn may be proved to be insufficient, unilateral and even erroneous—as all working-hypotheses may some time show themselves to be. But as yet it seems to be the most prosperous leading idea in genetics.

Heredity may then be defined as *the presence of identical genes in ancestors and descendants*, or, as Morgan says in full accordance with this definition: "The word heredity stands for those properties of the germ-cells that find their expression in the developing and developed organism."

And now it is time to end this communication, too long for its real contents, but too short for the importance and diversity of the great problem of heredity.

In concluding this address I must highly emphasize the eminent merits of Hugo de Vries. His famous book "*Die Mutationstheorie*," rich as well in positive indications as in ingenious views, has been the mediator for the new and the old era in genetics. This monumental work is a landmark in the progress of our science. Like the head of Janus it looks at once forward and backward, trying to reconcile—at least partly—the antagonistic ideas of continuity and discontinuity in evolution and heredity; hence a great deal of the charm of De Vries's work. But just these qualities have made the work of De Vries too eclectic for the stringent analytical tendencies of modern genetics—a tendency which has in recent years found a true home in American science.

## THE GENOTYPE HYPOTHESIS AND HYBRIDIZATION<sup>1</sup>

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It sometimes seems as if the hypercritical attitude had become an obsession among biologists. A proper judicial spirit is of course essential to science, but do not biologists often require a large amount of affirmative data before assenting to a proposition which is in reality a simple corollary of one already accepted?

For example, Darwin emphasized small quantitative variations as the method of evolution, although he recognized the occurrence of larger changes both quantitative and qualitative. De Vries, on the other hand, emphasized large variations—especially qualitative variations—as the real basis of evolution, although he too admitted the existence of lesser changes. He distinctly states that a mutation or new basis for fluctuating variation, may be so small that it is obscured by the fluctuations themselves.

If relative frequency of occurrence is a criterion of the value of variations in organic evolution, which is not necessarily so, Darwin's point of view is probably the nearer correct. If one could find a unit basis for describing variations in terms of the physiological economy of the organism concerned, *i. e.*, if one knew exactly what was a large change and what was a small change, he would probably find that a random sample of inherited variations followed the normal curve of error. By this I

<sup>1</sup> Read at the symposium on the "Genotype Hypothesis" at the meeting of the American Society of Naturalists, Ithaca, N. Y., December 28, 1910.

Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

The experimental results are from cooperative work between the Connecticut Agricultural Experiment Station and the Bussey Institution of Harvard University.

mean that small variations would center closely around a mode, and large variations would occur with a relative frequency inversely proportional to their size. The point that I wish to emphasize, however, is that neither Darwin nor De Vries recognized the proper distinction between a mutation and a fluctuation. Darwin made no distinction. De Vries, however, considered fluctuations to be linear; that is, to be limited to increase and decrease in characters already present. He thought that selection of such variations brought about changes in the selected population due to the inheritance of the fluctuations, but that the selected populations returned to the mean of the general population after selection ceased. Mutations, on the other hand, were gains or losses of entire characters—qualitative changes—which were transmitted completely, *i. e.*, were constant, from the beginning. De Vries did indeed state that mutations could take place in any direction, which would involve the idea of linear change or quantitative mutations; yet it seems quite evident from his general attitude in "*Die Mutationstheorie*" that to his mind qualitative and quantitative variations were quite distinct.

Many practical breeders had long known, however, that the selection of linear variations often produced new races which were as constant as any races, provided they were not exposed to crossing with individuals of the general population from which the selected race had come. Why this was true was unknown. It was felt that there was a real distinction between certain variations, to which Darwin had not called attention; yet it was felt that the De Vriesian idea was not wholly correct. It has been in making this distinction clear-cut and definite that Johannsen has rendered his great service. His elaborate extensions of the genotype conception of heredity have cleared up many debated points, and corroborative evidence has been received from so many lines that it can hardly be doubted that the main points of the hypothesis are correct. It may seem, therefore,

as if the superstructure of this conception were too elaborate to rest upon a simple foundation; yet I can not see but that the basis of the entire hypothesis is the fact that a fluctuation is a non-inherited variation produced upon the soma by environmental conditions, while the inherited variation, the mutation if you will, is any variation qualitative or quantitative, that is germinal in character. This being so, it seems scarcely necessary for an elaborate proof of the proposition, for it is nothing but a corollary to that part of Weismannism which was already generally accepted.

Of course it is recognized that pure Lamarckism still has followers to whom neither Weismannism in any form nor the genotype conception of heredity could appeal. But to thorough Weismannians and to those who believe in occasional germinal response to environmental conditions, it seems as if both propositions must be acceptable and their interdependence apparent.

Let us follow this line of reasoning to its logical conclusion in regard to the physiology of heredity. The Mendelian notation has been generally accepted as a convenient way of accounting for the facts of heredity in certain markedly discontinuous characters. It has been questioned by many, however, whether the Mendelian conception is not rather an apparent interpretation of a relatively small number of facts than a general law. De Vries has even suggested that there are definite physiological reasons why certain characters should Mendelize and others should not. His idea is that Mendelian segregation occurs when a germinal determinant for a character (*Anlage*) meets an opposing determinant, and when no such opposition exists the character in the cross-bred organism breeds true. Now the universal tendency of the facts of breeding is towards an interpretation the opposite of this. When a determinant from one parent meets with no such determinant from the other parent (presence and absence hypothesis), Mendelian segregation appears. When the same determinant is received from



both parents, segregation can not be proved, for the character breeds true.

In fact the many results of experimental breeding during the past few years have convinced me that De Vries's general conception of this matter is incorrect. There may be finally a considerable modification of our ideas regarding the ultimate nature of Mendelian unit characters and the exact meaning of segregation, yet the universal applicability of a strict Mendelian system to interpret the facts of heredity becomes more and more apparent every day. And the point that I wish to emphasize is that Mendelian inheritance is a genuine corollary of the genotype hypothesis if the latter is applicable to a population in a state of natural hybridity. In my work with maize where free intercrossing does occur I am convinced of the existence of genotypes in a state of natural hybridization. Furthermore, these genotypes can be isolated by inbreeding. If it were true, then, that only certain markedly discontinuous characters such as color Mendelize, how could genotypes which differ from each other in size characters be isolated? It is not expected, however, that the statement that Mendelian inheritance and the genotype hypothesis are interdependent will be received without proof. Data that are believed to furnish such proof are submitted here.

When Mendelism was a new idea it was natural that the behavior of many hybrids should be regarded as irreconcilable to such a system of interpretation. The earlier criticisms arose largely through the misconception that dominance instead of segregation was its essential feature. Later, when so many complex results from pedigree cultures were fitted into a strict and simple Mendelian notation, it was objected that the investigators could by expert juggling of a sufficient number of factors interpret according to their system any experimental results they might obtain. Perhaps a few biologists regarded as a personal affront the gradual growth of the idea that the facts of heredity were complex, but it is

hardly likely that many could regard this complexity as an invention of Mendelians. The latter would only too gladly have the facts as simple as possible.

There have remained, however, several instances in which hybrids apparently did not segregate in the  $F_2$  generation. Mendel himself investigated one such case, the genus *Hieracium*. The investigation of Ostenfeld<sup>2</sup> made this case perfectly clear by showing that the hybrids reproduced apogamously. Such asexual reproduction may also explain the behavior of hybrids between species of brambles which are also said to breed true in all their characters. These cases, however, and others among animals of which human skin color is the example *par excellence*, may be left out of consideration because no exact data concerning them have been forthcoming. There remain the experiments of two careful investigators who observed no segregation in the  $F_2$  generations of their hybrids, those of Lock<sup>3</sup> upon heights of maize plants and those of Castle<sup>4</sup> upon weights and ear lengths of rabbits. Lock expected that if segregation occurred it would be into two classes, *i. e.*, simple mono-hybridism. For this reason he made no measurements which would show whether he obtained the kind of segregation which as is shown later in this paper, does occur in maize hybrids. Castle<sup>5</sup> has recently admitted the possibility that his numbers were not large enough to prove definitely that segregation involving several small unit characters does not occur in the ear length of rabbits.

The difficulty attending this earlier work was that there was no way of explaining different manifestations of the same character. Segregating characters could always be interpreted either as the presence and absence of a unit

<sup>2</sup>Ostenfeld, C. H., 1904, "Zur Kenntnis der Apogamie in der Gattung *Hieracium*," *Ber. Deutsch. Bot. Ges.*, 22: 7.

<sup>3</sup>Lock, R. H., 1906, "Studies in Plant Breeding in the Tropics," III, Experiments with Maize, *Ann. Roy. Bot. Gard. Peradeniya*, 2: 95-184.

<sup>4</sup>Castle, W. E., *et al.*, 1909, "Studies of Inheritance in Rabbits," *Carnegie Inst. Wash. Pub.*, 114: 5-70.

<sup>5</sup>In lectures at the Lowell Institute, Boston, Mass., 1910.

giving a 3:1 ratio, or as the complementary action of two different units each allelomorphous to its absence, giving 9:3:3:1 ratios or modifications of them. Nilsson-Ehle<sup>6</sup> and the writer,<sup>7</sup> however, have shown that several units each allelomorphous to its own absence may be the determinants of what appears to the eye as a single character. In the above paper the writer suggested that if such ratios as 15:1 and 63:1—di-hybrid and tri-hybrid ratios, respectively—were found in considerable numbers, then higher ratios of this kind might account for the apparent constancy of hybrids in characters that seemed to be continuous. For, if—as is quite probable—the additional units increase the activity of the character in question, and if there is no dominance,<sup>8</sup> it is quite evident that hybrids may be intermediate between the two parents. All the pure classes in a complex character of this kind would indeed be difficult to isolate, but segregation could be absolutely proved by a comparison of the variability of the  $F_1$  and  $F_2$  generations.

Since writing the above paper I have obtained clear evidence of 15:1 ratios in two other cases. The first is a red pericarp color, the second is the condition of endosperm in maize which gives dented seeds as distinct from that which gives flinty seeds. There is even considerable probability that higher ratios occur which affect the latter character. In another paper<sup>9</sup> I have shown photographic evidence of size segregation in varieties of *Nicotiana rustica* and stated that similar evidence of segregation of size character in maize had been obtained. The following figures and tables show sufficient of the evidence from the maize crosses to demonstrate conclusively

<sup>6</sup> Nilsson-Ehle, H., 1909, "Kreuzungsuntersuchungen an Hafer und Weizen," *Lunds Universitets Årsskrift*, N. F., Afd. 2., Bd. 5, Nr. 2, 1-122.

<sup>7</sup> East, E. M., 1910, "A Mendelian Interpretation of Variation that is Apparently Continuous," *AMER. NAT.*, 44: 65-82.

<sup>8</sup> One dose, *i. e.*, receiving the same gene from a single parent, would on the average increase the manifestation of the character half as much as two doses.

<sup>9</sup> East, E. M., 1910, "The Role of Hybridization in Plant Breeding," *Pop. Sci. Mon.*, Oct., 1910, pp. 342-354.

that size characters segregate. It is hoped that this evidence will make us more cautious about accepting uncorroborated statements about characters which are definite exceptions to the Law of Mendel. It is by no means certain that no such exist, but no experimental proof of hybrids non-Mendelian in character has been made.

A further proof of segregation of size characters has recently been made in a preliminary note by Emerson.<sup>10</sup> He states that definite segregation occurs in beans, gourds, squashes and maize. His full data are therefore awaited with great interest.

Table I shows the frequency distribution of the heights of plants in a cross between no. 5 a medium-sized flint maize and no. 6 a tall dent maize. Sufficient seed was obtained in a previous season so that the entire series could be grown in rows side by side during one summer. This procedure eliminates any possibility that the variability of the  $F_2$  generation might have come from varying conditions of soil fertility.

It will be noticed that the  $F_1$  generation is nearly as tall as the taller parent. This increase in size is not due to dominance. It is the increased vigor that comes from crossing in maize, and while it obscures the hereditary differences in size, it is really a problem of development and not of heredity as was shown in a previous paper.<sup>11</sup>

The distribution of heights in the  $F_2$  generation is seen by simple inspection of the table to be more variable than the  $F_1$  generation in the case of each ear planted. Reduced to simple terms by the calculation of the coefficient of variation in each case, however, the two generations can be compared more accurately. In the  $F_1$  generation the  $C.V. = 8.68 \pm .553$  while in the various  $F_2$  generations from different ears the coefficients of variation run from  $12.02 \pm .559$  to  $15.75 \pm .684$ .

<sup>10</sup> Emerson, R. A., 1910, "Inheritance of Sizes and Shapes in Plants," *AMER. NAT.*, 44: 739-746.

<sup>11</sup> East, E. M., 1909, "The Distinction between Development and Heredity in Inbreeding," *AMER. NAT.*, 43: 173-181.

TABLE I<sup>12</sup>  
FREQUENCY DISTRIBUTION OF HEIGHTS OF MAIZE PLANTS IN CROSS (5 × 6)

No.	Class Centers in Inches for Heights of Plants																			A.	S.D.	C.V.			
	51	54	57	60	63	66	69	72	75	78	81	84	87	90	93	96	99	102	105				108	111	
5	3	2	4	5	11	17	17	18	10	6	4												68.22 ± .406	6.49 ± .324	9.51 ± .421
6																							101.18 ± .400	5.07 ± .283	5.01 ± .279
(5×6)-F <sub>1</sub>																							94.53 ± .740	8.21 ± .519	8.68 ± .553
(5×6)-1F <sub>2</sub>	2	1	3	6	3	5	10	10	22	16	10	7	11	13	6	10	8	4	4	2	2		81.00 ± .685	12.76 ± .486	15.75 ± .684
(5×6)-2F <sub>2</sub>							4	2	6	5	12	8	12	6	5	8	3	10	8	2	2		88.33 ± .802	11.78 ± .567	13.34 ± .675
(5×6)-3F <sub>2</sub>																							79.46 ± .621	9.55 ± .438	12.02 ± .559
(5×6)-8F <sub>2</sub>	2				4	4	12	7	9	13	12	15	10	8	8	1	1	1	1	1	1		79.46 ± .621	9.55 ± .438	12.02 ± .559
(5×6)-14F <sub>2</sub>	1	2	4	2																			81.24 ± .513	10.28 ± .364	12.65 ± .450

TABLE II<sup>13</sup>  
FREQUENCY DISTRIBUTION OF HEIGHTS OF PLANTS IN CROSS (54 × 60)

No.	Class Centers in Inches for Heights of Plants																							Total	
	22	25	28	31	34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88		91
No. 54																									
(60-5 x 54) F <sub>1</sub>																									
(60-8 x 54) F <sub>1</sub>																									
(60-3 x 54) F <sub>1</sub>																									
(60-5 x 54) F <sub>2</sub> <sup>15</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>16</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>17</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>18</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>19</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>20</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>21</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>22</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>23</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>24</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>25</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>26</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>27</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>28</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>29</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>30</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>31</sup>																									
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(60-8 x 54) F <sub>2</sub> <sup>37</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>38</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>39</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>40</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>41</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>42</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>43</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>44</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>45</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>46</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>47</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>48</sup>																									
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(60-5 x 54) F <sub>2</sub> <sup>84</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>85</sup>																									
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(60-3 x 54) F <sub>2</sub> <sup>89</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>90</sup>																									
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(60-5 x 54) F <sub>2</sub> <sup>99</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>100</sup>																									
(60-3 x 54) F <sub>2</sub> <sup>101</sup>																									
(60-5 x 54) F <sub>2</sub> <sup>102</sup>																									
(60-8 x 54) F <sub>2</sub> <sup>103</sup>																									

<sup>12</sup> Grown side by side in same season.

<sup>13</sup> Distributions giving figures grown side by side in same season.

<sup>14</sup> Extremes were measured and number of plants counted. All were strongly convergent around the central classes.

<sup>15</sup> Grown from five different ears.

<sup>16</sup> Grown from two different ears.

<sup>17</sup> Grown from three different ears.

Table II shows a similar distribution of heights in cross between no. 60, a dwarf pop maize commonly known as Tom Thumb, and no. 54, a sugar corn known as Black Mexican. The distribution of heights of no. 54 was obtained in the same season as the  $F_2$  generation. They were both grown upon the same plot of ground in which the soil appeared to be quite uniform. Unfortunately, the exact distribution of the heights of no. 60 and of the  $F_1$  plants which were grown in previous seasons, is unknown. The range of the variates shown by the black lines, however, is correct. Furthermore, from notes recorded at the time we know that the  $F_1$  generation was comparatively uniform, the greater number of variates being distributed around classes 67, 70 and 73 inches. In this case, also, the effect of crossing is shown by the relatively high plants of this generation. The plants of the  $F_2$  generation show a wide range of variation. The highest individuals are practically the height of the highest individuals of the taller parent, no. 54. The lowest plants of  $F_2$  do not reach the lower range of no. 60. I interpret this as due to continued heterozygosis in other characters and to physiological correlation. By the latter term I mean that since the plants of no. 60 are very small,  $F_2$  segregates of the same size could only be expected where the ears and seeds also are very small. But since the ears and seeds of these plants also show segregation in new combinations, normal growth correlation probably resulted in a somewhat larger average size. For example, little 40-inch plants were found with ears three times the length of normal ears of no. 60. It is likely that such plants might have been smaller if they had been recombined with the characters necessary for the production of smaller ears.

Table III and Figs. 1-4, show the lengths of ears in the cross just described. In making this table the best ear from each plant that bore a well-filled ear was taken. The small ears, therefore, do not represent poor, unfilled or supernumerary ears. The coefficients of variability



TABLE III<sup>18</sup>  
FREQUENCY DISTRIBUTION OF LENGTHS OF EARS IN CROSS (60 X 54)

No.	Class Centers in Cm. for Lengths of Ears																	A.	S.D.	C.V.
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21			
No. 60	4	21	24	8														6.6 ± .073	.81 ± .051	12.27 ± .783
No. 54																		16.8 ± .121	1.87 ± .088	11.13 ± .531
(60-5 x 54) F <sub>1</sub> <sup>19</sup>					1	12	12	14	17	9	4							12.1 ± .121	1.51 ± .088	12.48 ± .722
(60-5 x 54) F <sub>2</sub> <sup>20</sup>		4	5	22	56	80	145	129	91	63	27	17	6	1				12.7 ± .058	1.99 ± .037	15.67 ± .296
(60-8 x 54) F <sub>2</sub> <sup>20</sup>		1	10	19	26	47	73	68	68	39	25	15	9	1				12.9 ± .076	2.25 ± .053	17.44 ± .413
(60-3 x 54) F <sub>2</sub> <sup>21</sup>		2	5	17	33	33	33	27	21	13	10	11	12	1	2	1		12.6 ± .128	2.81 ± .087	22.30 ± .744

TABLE IV  
FREQUENCY DISTRIBUTION OF WEIGHTS OF SEEDS OF CROSS (60 X 54)

No.	Class Centers in Grams for Weights of 25 Seeds																				A.	S.D.	C.V.	
	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5				
	7	22	28	4																				
60																					2.7 ± .034	.31 ± .024	14.44 ± .899	
54				5	12	13	17	4	3	2	2	5	7	14	10	5	4	1	2	1	2	8.3 ± .107	1.21 ± .074	14.54 ± .963
(60-5 x 54) F <sub>1</sub> <sup>22</sup>																					4.6 ± .059	.64 ± .041	13.91 ± .912	
(60-5 x 54) F <sub>2</sub> <sup>23</sup>	1	7	17	49	98	113	83	69	43	27	13	8	1	1			1				5.3 ± .032	1.09 ± .022	20.56 ± .442	
(60-8 x 54) F <sub>2</sub> <sup>23</sup>			1	3	15	16	17	23	23	18	12	8	9	1	1						6.2 ± .067	1.23 ± .047	19.84 ± .799	
(60-3 x 54) F <sub>2</sub> <sup>24</sup>				4	10	24	41	53	40	52	21	19	9	8	2	3					6.0 ± .047	1.17 ± .033	19.50 ± .563	

<sup>18</sup> No. 60 and F<sub>1</sub> gen. grown in 1909, No. 54 and F<sub>2</sub> gen. in 1910.

<sup>19</sup> Grown from five ears.

<sup>20</sup> Grown from two ears.

<sup>21</sup> Grown from three ears.

<sup>22</sup> Grown from five ears.

<sup>23</sup> Grown from two ears.

<sup>24</sup> Grown from three ears.

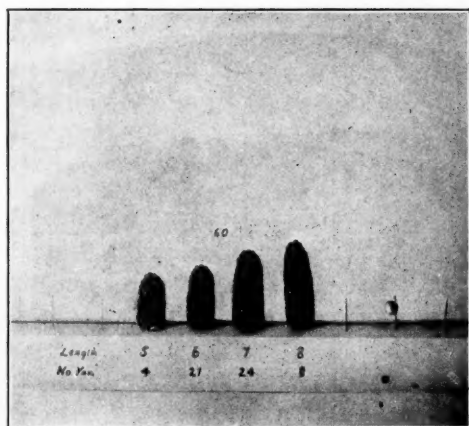


FIG. 1. No. 60, female parent, illustrating variation in length of ear ( $\frac{1}{8}$ ).

have again been calculated, but they hardly emphasize the real segregation as well as do the photographs which were made from representative ears of the different classes found in the actual crop.

Table IV shows the segregation of weights of seeds in  $F_2$  in this same cross. Fig. 5 shows the average size of

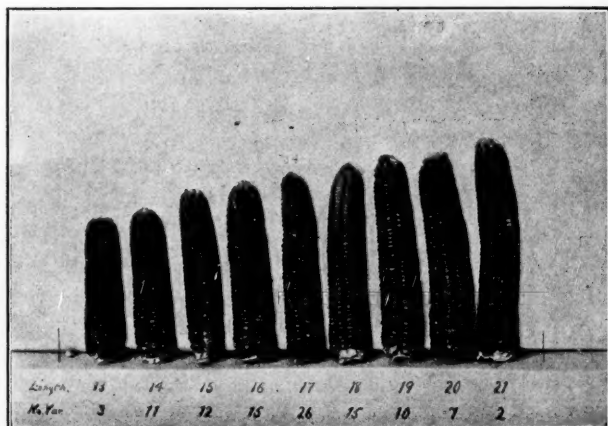


FIG. 2. No. 54, male parent, illustrating variation in length of ear ( $\frac{1}{8}$ ).

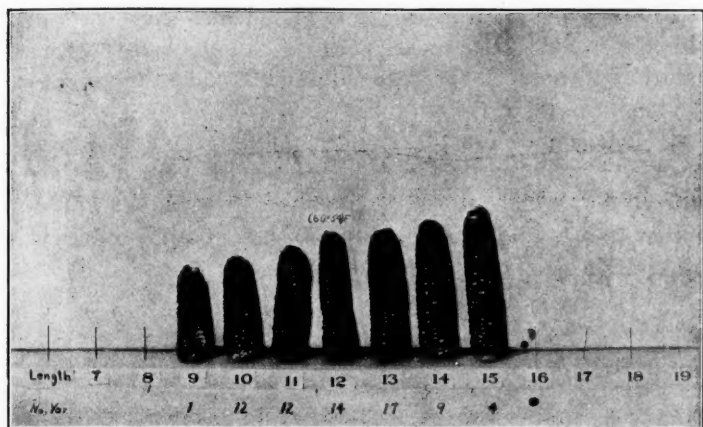


FIG. 3. Variation in length of ear of  $F_1$  generation of cross between No. 60 and No. 54 ( $\frac{1}{8}$ ).

the seeds of the two parents and the  $F_1$  generation and the extremes of the  $F_2$  generation. In making the weights for this table, it was necessary to use a scheme by which the sugary wrinkled seeds of the Black Mexican parent, no. 54 could be weighed as starchy seeds. This

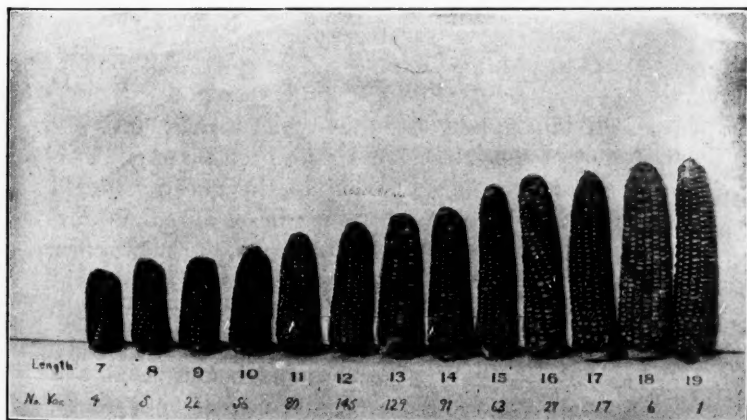


FIG. 4. Variation in length of ear of  $F_2$  generation of cross between No. 60 and No. 54 ( $\frac{1}{8}$ ).

was done by planting the no. 54 between rows of the hybrid. Sufficient crossed seeds which had become starchy through *Xenia* were obtained to make the weights given. Not all of the ears, however, had 25 starchy seeds, which accounts for the small number of plants measured. Furthermore, the seeds of no. 54 were a rather mixed lot, which of course resulted in a higher variability than would probably have been found if only seeds

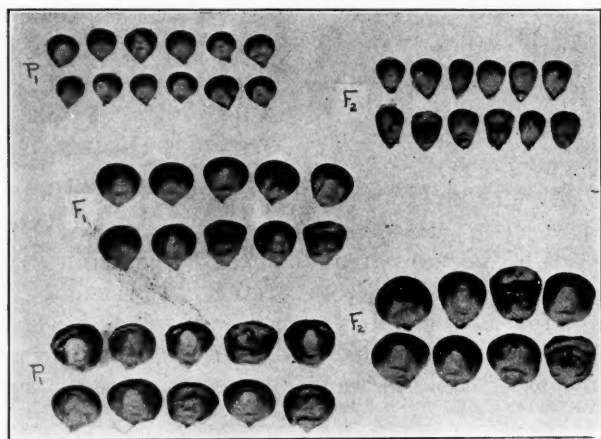


FIG. 5. Average size of seeds of No. 60 and No. 54 and the  $F_1$  generation of the cross between them. Extremes of the  $F_2$  generation.

of the individual plant of no. 54 which was used as the male parent of the cross, could have been planted. Perhaps it should be noted here since the question might arise, that since the size of the seeds on an ear is governed by the development of the pericarp, the sugar corn, no. 54, was unaffected in other ways than by having the pericarp filled out with starch by the hybridization which occurred attended by the resultant *Xenia*.

In Tables III and IV the measurements and weights of the  $F_1$  generation were recorded from only one cross, although three crosses between the two varieties were made. It might be said that one has the right to com-

pare only the  $F_2$  generation of cross of which the  $F_1$  generation is given. If this were granted our conclusions in regard to segregation would be the same. It might be said, however, that sufficient records were made of the  $F_1$  generations of the other crosses to know that they differed but little from the family of which the data were recorded. In addition, it is a fact that general

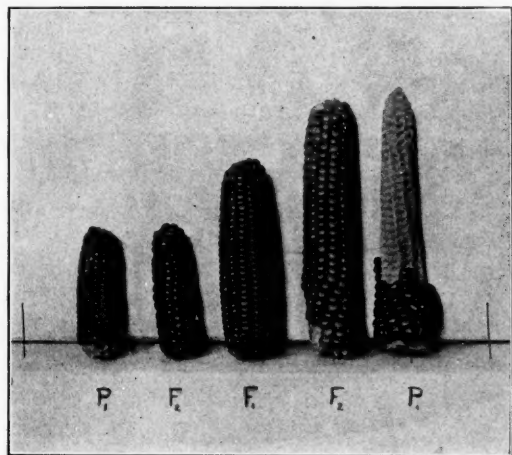


FIG. 6. Average ears of No. 60 and No. 58 and the  $F_1$  generation of the cross between them. Extremes of the  $F_2$  generation.

populations of the two parents were studied, and their variation was undoubtedly greater than would have been that of the inbred progeny of the three parent plants of either variety.

An additional cross between Tom Thumb pop maize and a small purple flint is illustrated in Fig. 6. The ears pictures show the average size of the two parents and the  $F_1$  generation, and extremes of the  $F_2$  generation.

In conclusion there are two points I wish to notice. Unquestionable segregation in size characters has been shown by comparison of the  $F_1$  and  $F_2$  generations. It can scarcely be doubted that some of these segregates will breed as true as the parent forms, yet one can

scarcely do more than speculate in regard to the specific characters that are concerned in developing either organs or individuals of certain sizes. There are probably many characters that interact together in developing certain characters, although the actual determinants in the germ cells may be transmitted independently. These interdependent reactions during development obscure to us the real causes and what we regard as independent characters may be but indirect results of unknown causes. For example, the ability to evert their starch when heated has been the distinguishing character of the subspecies called *Zea mays everta*, the pop maizes. This character so called, however, is the resulting physical condition of the starch caused at least partially by the small size, the thickness and the toughness of the enveloping pericarp.

For these reasons it may not be possible—at least very soon—to point out even the number of characters concerned in size developments. From the number of extreme segregates obtained in each case I might venture to state that the size of ear in the cross shown in Fig. 5 is apparently due to not less than three characters, while the size of ear in the other cross pictured seems to be due to not less than four characters.



## NOTES ON GUNDLACHIA AND ANCYLUS

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ABOUT seven years ago,<sup>1</sup> in the *Nautilus* I called attention to certain problems connected with the genera mentioned in the title of this paper, and urged investigation of the subject from the hypothetical view of the two following propositions:

1. That *Gundlachia* is merely an *Ancylus* which under favorable circumstances has been able to form a calcareous epiphragm and survive the winter, which ordinarily kills the great mass of individuals, and, while retaining the shell of the first season, to secrete an enlarged and somewhat discrepant continuation of it during the second summer.

2. That not all Ancyli necessarily have the ability to do this, but the practise may have developed in certain small species; and in tropical regions where the dry season takes the place of winter it is possible that survival may become more or less habitual with some of these species.

In this connection attention may be recalled to the aestivation in dry mud behind a double epiphragm, in the Bahamas, of *Segmentina dentata* Gould,<sup>2</sup> and to the observations of Erland Nordenskjöld<sup>3</sup> on *Ancylus moricandi* Orbigny, in Brazil.

During the past four years I have received an interesting series of notes by Mr. John A. Allen, of Cleveland, Ohio, connected with the Nungesser Electric Works of that city, who has for some time been domesticating in small aquaria species of fresh-water shells, including

<sup>1</sup> *Nautilus*, XVII, No. 9, pp. 97-98, January, 1904.

<sup>2</sup> Smithsonian Miscell. Coll., Vol. 47, Pt. 4, No. 1566, pp. 446-448, April, 1905.

<sup>3</sup> *Zool. Anzeiger*, XXVI, pp. 590-593, July, 1903.

*Ancylus* and *Gundlachia*. His observations extend over some six years and his notes contain so much of interest that it has seemed desirable to summarize and publish his data, thus placing on record facts which may stimulate others to follow his example.

Mr. Allen was kind enough to send to the museum a lot of *Anacharis* supposed to contain both *Ancylus* and *Gundlachia* in the living state, and numerous specimens of the former were observed in a jar to which the vegetation was consigned, immediately after it was filled with water. We were not able to distinguish with certainty any *Gundlachia*, though some may have been present, and the small aquarium was kept in good condition to await developments. This was in December, 1907. The *Ancyli* continued to exist in apparent health during the winter. In May, 1908, they seemed to go into hiding, but during the summer reappeared again in rather diminished numbers, while a few young ones were observed. No particular change was noticed during the following winter and spring. While absent during the summer of 1909, it became necessary to transfer the collections to the new building of the National Museum and the aquaria were set aside. After the confusion of the transfer was measurably over, I examined the aquaria and, finding nothing visible, had the contents of the smaller one (about  $8 \times 4 \times 10$  inches in size) removed and submitted to the most careful scrutiny, the sand at the bottom being placed in a fine sieve for examination, but not a trace of *Ancylus* remained. I concluded that there had been sufficient carbonic acid in the water to completely dissolve these fragile shells after death, and that some unfavorable condition had exterminated the colony. In the other aquarium, which was about eight times the capacity of the smaller one, the water had evaporated to about half its normal quantity and no mollusks except a few small *Lymnæas* were visible, while the *Anacharis* had suffered considerably by the adverse conditions. This was towards the end of November, when it was

difficult to get any fresh weed except by purchase. Being much occupied, I contented myself with having the aquarium filled with Potomac water from the tap. A short time afterward I was surprised to note a large number of young *Ancylus* with clean translucent shells, on the side of the tank. There had never been any *Ancylus* in the aquarium except such as might have been put in with Mr. Allen's *Anacharis*. These had up to February 22, 1910, grown rapidly and continued to flourish, though the number then visible was only about half that which was noticed in November. In April the *Ancylus* completely disappeared again. I have not been able to discover where they went to, as the most careful scrutiny of the sparse amount of *Anacharis* remaining has not revealed any on the stems or leaflets. None of the specimens seemed to have formed any septum and nearly all of them were carrying a small colony of five or six minute hydroids on the posterior upper surface of the shell. The shells in February were still too fragile to admit of removal from the glass without crushing, and most of them kept on the side away from the window, on the sill of which the tank stood. They were about 3.0 mm. in length, and remarkably active, moving about on the glass with surprising speed.

Subsequently Mr. Allen kindly furnished me specimens of all these stages in alcohol; and I also had the opportunity of seeing some specimens in alcohol which had been sent to Mr. Bryant Walker and Dr. H. A. Pilsbry in 1908, and which were obviously identical with those sent as examples by Mr. Allen to me over a year later, and Dr. Pilsbry thought also with specimens collected at Rockford, Illinois, in the ancyloid stage. On account of its relations to the *Gundlachia* it will be referred to here as *Ancylus meekiana*, since, unless in the *Gundlachia* stage, it seems not to have been described.

Mr. Allen also sent a lot of the wild *Ancylus* collected in the Thornburg lagoon and which he was disposed to regard as something distinct from his aquarium ancy-

loids. After a careful examination under the microscope I have been unable to find any constant differences between shells of the same age, except that the larger specimens of *Ancylus* seem to have grown continuously and evenly, while those ancyloids which attained a *Gundlachia* stage show the sharp contrast between the separate stage and that with the expanded third stage of the shell. As this is only what one might expect if the *Ancylus* attained its full growth without interruption, while the ancyloid becoming septate passed through a resting stage and then began to grow again, I consider this difference of no moment systematically. The young *Ancylus* and the ancyloid of the same length appeared generally quite identical, though I noticed that in both the obliquity of the apex varied to some extent, being more emphatically bent toward the posterior right side in some individuals than in others.

*Ancylus meekiana* is, when young, for a time nearly parallel-sided, the growth toward maturity being more expanded than at first. The apex is behind the middle of the shell and slightly inclined toward the posterior right-hand side at maturity. The microscope reveals some very feeble radial striæ from the apex, mostly vanishing before they reach the base. The incremental lines are not strongly marked and the shell when clean is of a pale translucent yellowish color. At or near maturity the shell assumes a more oval form slightly more expanded in front than behind. The animal has short pointed tentacles, well-marked black eyespots, and a bluish-white color, except about the mouth, where the yellow-brown jaws are laterally set and the buccal mass has a pinkish color. The shell is about 3.6 mm. long, 2.3 wide, and 1.0 high. In the dark-colored specimens of the wild *Ancylus*, on the inside, may often be seen a dark-brown line corresponding to the margin of the young *Ancylus* and showing the more parallel-sided early outline.

Miss Mary Breen, who has been studying the anatomy of the fresh-water gastropods of the District of Co-

lumbia, was kind enough to undertake the removal and mounting of radulæ taken from specimens of the different stages, as well as from the wild *Ancylus*. This was a task of no little difficulty on account of the extremely minute size of the organ. The radulæ of ancyroids, septates and *Gundlachia* were absolutely identical in appearance and in number of teeth, the formula 5·10·1·10·5, holding good for all. The uncinial teeth are not gradually modified from the laterals, but change abruptly and form a distinct band on each side of the radula. The lateral part of Stimpson's figure of the dentition of his *Gundlachia meekiana* is imperfectly made out, and obviously inaccurate; due doubtless to the fact that he had only a few specimens and a not very powerful microscope. Unfortunately his original material was destroyed in the great fire at Chicago of 1871.

An examination of the radula of a septate form, collected in Nicaragua by Professor B. Shimek, showed a similar radula but with one more uncinial tooth on each side. In this case, unfortunately, while endeavoring to transfer the minute object to a slide for permanent preservation, it mysteriously disappeared, and a trial with a second specimen was no more successful.

The form of the laterals is fairly well given by Dr. Stimpson, and the rhachidian tooth is correct in his figure; but the gradual modification and uncertain number of the outer teeth of the radula do not agree with our observations on the specimens from Ohio. Renewed correspondence with Mr. Allen led to the preparation of this paper, pending the continuation of his observations.

Since the different stages of *Gundlachia* need to be carefully discriminated, I have adopted the following nomenclature for them.

In the first stage, when the young shell has a laterally compressed subconical shape without any trace of septum, and is to all intents and purposes, concholog-

ically and anatomically, an *Ancylus*, I call the individuals "ancyloids."

In the second stage when the base of the conical shell is more or less closed by a flat horizontal septum continuous with the margin around it, I call the individuals "septates."

Lastly, when the animal in its second season begins to form a marginal expansion external to the septum, and with its longitudinal axis sometimes at a considerable angle with the axis of the ancyloid shell, I reserve for this stage, up to and including maturity, the term "*Gundlachia*."

Mr. Allen kindly sent alcoholic specimens of ancyloids, septates and *Gundlachias* from his aquarium for anatomical examination. The posterior part of the foot entirely hides the septum when the living animal on the walls of the aquarium is examined through the glass. Nothing to distinguish it from ordinary *Ancylus* is visible in the soft parts. The creatures feed on the microscopic algæ, etc., which grow on the walls of their domicile and when feeding the movement of the jaws and radula can be seen with ease by means of a magnifier. On the alcoholic specimens, on the exterior of the shell, were many minute lenticular capsules which, from analogy with *Neritina*, *Pompholyx*, etc., were supposed to be the ovicapsules. The very young shells are very transparent and fragile. It is difficult to find them until they have reached a length of over a millimeter, and so far it has proved impracticable to detach them from their roost without crushing them, they are so extremely fragile. The smallest septate seen was slightly less than two millimeters in length and the animal had entirely withdrawn behind the septum, which covers more than two thirds of the aperture.

The species in the *Gundlachia* stage agrees substantially with the form described from the District of Columbia by Stimpson, under the name of *Gundlachia meekiana*. As in many other fresh-water shells the newly



formed shell is yellowish translucent, while the older part, especially when the pond or aquarium has a muddy bottom, often becomes darkened or even blackish, and more or less covered by a growth of conferva. Mr. Allen calls attention to the fact that the sharp line of demarkation which separates the dark encrusted shell of the septate from its translucent *Gundlachia* extension in the final stage, is evidence that the growth is not continuous, but that a resting period of some duration separates the two stages.

I have preferred for the most part to refrain from theorizing on the inferences to be drawn from the data, letting them speak for themselves. To me, however, the facts tend strongly to confirm the hypothesis suggested in the opening paragraphs of this paper.

#### GENERAL NOTES

The following notes are partly summarized from a rather voluminous correspondence with Mr. Allen, extending over more than four years.

The Thornburg lagoon is an abandoned channel of the Cuyahoga River. In 1903 the river was fairly well stocked with Unionidæ, but soon after that date the contamination of the river by drainage and sewage killed off the naiad population. This contamination is not believed by Mr. Allen to have seriously affected the water of the lagoon, though for some reason it does not seem to be a place favorable to vigorous growth of mollusks. It produces a dwarf *Planorbis parvus*, a poorly developed *Physa*, a small form of *Lymnæa humilis modicella* and a scanty supply of *Amnicola*. It is nearly filled with *Nuphar* on the leaves of which *Ancylus* is found; also *Ceratophyllum*, *Potamogeton*, etc., occur, especially where the water is shallow.

At one place the bank bordering on the lagoon is steep and the water near it deep, so here even at low water mollusks would never be left dry. There is another portion of the lagoon where a wide zone, producing vegeta-

tion on which *Ancylus* occurs, is sometimes left uncovered when by dry weather the water becomes low. In this part of the lagoon three *Gundlachia* were found. In general the water of the lagoon is deep and constant, but owing to the presence of these shallows the hypothesis that the formation of a septum in *Gundlachia* may be due to alternation of wet and dry periods can not be wholly excluded.

*Ancylus* occurs in one to three feet of water where *Ceratophyllum* is abundant. In the deeper water shore there is more *Nuphar* and less fine vegetation the *Ancylus* seems to be absent or rare.

Mr. Allen attempted to domesticate the Thornburg *Ancylus*, placing many young ones in a 15 × 9-inch jar stocked with *Anacharis* from the lagoon. Apparently, all soon disappeared, although *Lymnæa* and *Amnicola*, coincidentally transferred, lived a long time.

#### NOTES ON THE SEVERAL JARS USED AS AQUARIA

*The 15 × 9-inch Jar.*—This originally contained a dwarf *Nymphaea* which died. There was a mixture of peaty and ordinary soil about three inches deep in the bottom of the jar. This was stocked in 1906 with *Anacharis* and some specimens of *Vivipara*. The date of the first appearance in it of the ancyloid stage of *Gundlachia* was not determined. February, 1907, individuals were very numerous and, some being taken out to save in the dry state, the septate form was discovered. Mr. Allen had noticed the presence of the ancyloid form some time before. The first date at which *Gundlachia* had been obtained from the Thornburg lagoon was July 15, 1906, but Mr. Allen doubts if the copious swarm of ancyloid individuals of *Gundlachia* could have originated in the jar so quickly from individuals accidentally put in at that time. Some of the vegetation in the jar had been received from elsewhere in Ohio, and some from another state. The ancyloid stage of the *Gundlachia* can not be distinguished from the associated *Ancylus* by

the external features as seen in the aquarium. In February, 1907, probably hundreds of the unseptate ancyloid form were present. There were several *Vivipara* in the jar that winter. Subsequently they were removed, Mr. Allen thinking that they might consume the food supply needed by the ancyloids. Having heard that the stunted growth of aquarium mollusks might be due to the presence of their soluble excreta in the water, he thought the removal of the *Vivipara* might have had some influence in this way. However, the removal of the large snails did not stop septation.

In the winter of 1906-07 the specimens of *Planorbis parvus* in the jar were large and healthy. In the winter of 1907-08 the individuals of this species appeared dwarfed. The water in the jar was then removed and replaced by distilled water. After that the *Planorbis* (and Mr. Allen thought also the *Anacharis*) took on a more healthy appearance. He thought that the concentration of saline matter due to refilling loss from evaporation with ordinary lake water might have been influential injuriously, and the transfer to distilled water have lessened the tendency to septation.

In the winter of 1907-08 septate individuals of which the exact number were not recorded were again found in the jar. In January and February, 1908, the ancyloid form was fairly plenty, though not so numerous as in the previous year. In spring they became fewer and in May, 1908, there were none visible (although in a smaller jar there were some). They reappeared in the first half of June, 1908. July 3, 1908, an immature septate individual was taken, and another on July 20. On the theory that the septum is formed during a resting stage, these may have been forming during May, when nothing was in sight. August 3, 1906, another specimen was taken. January 11, 1909, a specimen was found which had begun to add the third or expanding stage of the shell external to the septum. No mature *Gundlachia* were taken from this jar during the winter of 1908-09.

August 19, 1909, a minute ancyloid specimen was taken, and another August 24. September 26 six ancyloids were visible at one time, but were not disturbed. It was noticed that the ancyloids came out in sight on the walls of the jar more freely on cloudy than sunny days.

This jar, December, 1909, contains a dense and vigorous growth of *Anacharis*, also plenty of fresh-water algæ. It stands in the factory room subject to the fall of factory dust, and to the changes of temperature in the room. When the room gets unusually cold the ancyloids mostly retire out of sight, temporarily. December 9, 1909, two specimens with the third stage of the shell partly grown were taken near the top of the jar. A sudden spell of unusually cold weather having begun two nights previous may account for the ancyloids having gone, as they did, into hiding, but it was somewhat surprising that the more nearly mature form had not also hidden.

*The 8 × 6-inch Jar.*—This had sand on the bottom and was planted with *Anacharis* from the larger jar, carrying with it *Ancylus*, *Gundlachia* and *Planorbis parvus* in the summer of 1908. The following winter, having nothing but sand and water to live on, the vegetation had become rather attenuated and feeble looking. The ancyloids were few and perhaps not more than half as large as those in the larger jar. January 19, 1909, two or three immature septate specimens were taken from this jar, and February 10 one about half grown. Very few ancyloids were seen about this time in this jar. February 11 two immature septate specimens were taken, being all of either form which were at that time visible. February 24, 1909, for the first time since the eleventh, a small ancyloid was noticed. On the twenty-seventh one moderate-sized but fully septate individual was taken and one ancyloid seen. Another septate was taken March 8, and March 11–13 a solitary ancyloid was noticed.

Fearing that there was not enough stock in the jar to

continue the race, March 15, Mr. Allen put in half a dozen ancyloids from the large jar. March 29 a mature septate was taken out, and it was noticed that the *Planorbis* looked frail as if insufficiently supplied with lime salts. October 11, 1909, two half-grown septates were taken from this jar. In the winter (1909-10) the *Planorbis*, for some unknown reason, completely disappeared.

From these data Mr. Allen concludes that about 80 per cent. of the stock in this jar had assumed the septate form, the conditions obviously being such as to stunt both *Anacharis* and ancyloids. In the 15 × 9-inch jar the vegetation is luxuriant and abundant, and the septate individuals produced were only about two to five per cent. of the ancyloids. From this Mr. Allen concludes that the formation of a septum is promoted by causes which tend to restrict or retard growth.

*The 9 × 7-inch Jar.*—This has a mixture of sand and soil at the bottom. There is plenty of algal growth, but the *Anacharis* is not as vigorous as in the 15 × 9-jar, from which it was stocked with ancyloids and *Planorbis*. In the winter of 1906-07 it yielded two septates. The winter of 1907-08 ancyloids were fairly numerous, more so than during the first winter, but no septates were detected. July 1, 1908, young fry, hatched that season, were visible. March 8, 1908, a fine large mature *Gundlachia* was taken. The original ancyloid part was deep black and the flaring expansion beyond it was colorless and transparent. In the sand-bottomed jar the mature *Gundlachia* is uniformly yellowish translucent, but in the large jar with mud bottom the whole shell gets blackish. December 13, 1909, a census of this jar was attempted. The day was dark and a count difficult, but the result was six septates and two ancyloids, all eight being small and immature.

*A Jar without Planorbis.*—Thinking it might be desirable to have a stock of the ancyloids not associated with *Planorbis*, Mr. Allen, about February, 1909, when

the *Planorbis* was not breeding, transferred some *Anacharis* and a number of mature ancyloids to a new 15 × 9-inch jar, taking care not to introduce any *Planorbis*. May 3, 1909, the first ancyloid hatched in the jar was noticed; it was about half the size of the parents. Others appeared later. By December, 1909, the parent stock had disappeared and the stock hatched in the jar remains very small, indicating some unfavorable condition. The bottom of the jar was covered with a mixture of ordinary and swamp soil, but the supply of swamp soil used in previous jars having been used up, that in the present jar was taken from another place, and may have contained some unfavorable matter. The *Anacharis* in the jar is fairly flourishing, but there is no green algal growth.

*General Conclusions.*—The *Gundlachia* may reproduce before assuming the completely mature form. The shell varies in apparent color in accordance with the muddy or sandy character of the bottom soil, but the dark coating in the former case is not incorporated with the shell structure.

The ancyloid stage has a period of least activity in May. In July and August the septates appear. In autumn and early winter the third stage is developed, becoming mature and complete in February or March. This course is, however, not invariable in the aquarium or domesticated specimens, since Mr. Allen has taken ancyloids in January or February, an irregularity probably due to temperature and which might not have occurred in specimens under perfectly natural conditions. It is not certain that the ancyloids detected by Mr. Allen in July and August were the young of that season, since the minute creatures are very difficult to detect in the aquarium and can not be handled. They are so translucent in the younger stages as to be practically invisible. However, it is probable that the eggs are laid during the winter and hatched in the very early spring.

It seems likely that under average conditions only a



small proportion of the individuals advance beyond the septate stage; and also that, of the ancyloids, only part reach that stage. It is also probable, from Mr. Allen's observations, that anything which tends to retard development may coincidentally increase the tendency to form a septum.

Since there is a period of least activity in May, a natural observation year will be from one May to another. Mr. Allen summarizes the results obtained during the period, May, 1908, to May, 1909, as follows:

None being taken before July nor after the following March, there were secured between July, 1908, and March, 1909, inclusive:

15 × 9-inch jar 4 septates	} total 15.
9 × 7-inch jar 1 septate	
8 × 6-inch jar 10 septates	

From August 19, 1909, to December 13, 1909:

15 × 9-inch jar 8 septates	} total 16.
9 × 7-inch jar 6 septates	
8 × 6-inch jar 2 septates	

Further correspondence, during February, 1910, affords additional notes.

A lot of the wild Thornburg *Ancylus* in alcohol was sent by Mr. Allen and, contrary to his expectation, on careful comparison with his series of ancyloids from his aquaria, no difference, beyond slight individual variations, could be observed in the shells of the two series, while the radula and the soft parts, after repeated comparisons, seemed to be identical in both.

Mr. Allen especially notes that in the winter, 1909-10, the septates were the prevailing form in his aquaria, exactly the reverse of the case when the aquaria were freshly established. The generation, which appeared in May and June, 1909, in the "*Planorbis*-free" jar, was dwarfed was not in sight during the latter part of the winter, 1909-10, and may possibly have all died. Mr. Allen attributes the poor success of this jar to the use of

swamp soil from a different place from that previously used.

February 15, 1910, being a dark day and therefore favorable for the septates to be out of sight, Mr. Allen counted those visible in the large aquarium. Six septates and one ancyloid were noted. This illustrates the observation that (excepting the "*Planorbis*-free" jar) the septate is the prevailing form this season, and is promoted by causes which dwarf or retard growth.

After noting the inexplicable way in which fresh-water mollusks sometimes appear and disappear from pools where they occur, Mr. Allen further suggests that the septate form may be a prelude to total disappearance of the species from a given place.

Another count on February 17, 1910, gave three ancyloids and three septates in sight, which Mr. Allen remarks is the first time for a considerable period that the two forms have appeared in equal numbers. In the large jar every mature specimen seen this season has been conspicuously bicolored, the ancyloid or septate part being stained deep black, while the flaring extension is translucent and colorless, indicating that a resting period intervened between the completion of the septum and the formation of the mature shell.

Three ancyloids seen February 17 were all translucent and about the same size. There can be little doubt that they date from the summer of 1909. Hence, Mr. Allen infers that the blackened original shells of the mature *Gundlachia* date from the season previous.

TABLE FOR JANUARY AND FEBRUARY, 1910

*Specimens taken or observed*

Date	<i>Gundlachia</i>	Septates	Ancyloids
January 12 (big jar) .....	1	1	0
January 19 (big jar) .....	1	0	0
January 31 (small jar) .....	1	0	0
February 4 (big jar) .....	2	0	0
February 5 (big jar) .....	3	1	0
February 6 (medium jar) .....	0	2	0

My last communication from Mr. Allen, dated December 11, 1910, contains the following additional notes:

As I have already written there was plenty of A-form (ancyroids) and no G-form (septates) visible in my original large jar last summer. But, since the latter part of November, besides ancyroids in various stages, young septates have been visible in fair abundance. I counted about a dozen in sight at one time.

He concludes that ancyroids are present most of the year, but only young ones in May and mostly also in June. But septates appear to be a strictly winter form, that is, the immature septate stage appears in August or later, reaches maturity (*Gundlachia*) in February or March, and disappears about the end of April, after which and a shorter or longer interval the young ancyroids of the season begin to appear in the jars.

If the hypothesis stated at the beginning of this paper be well founded, it would explain why mature *Gundlachias* appear, if at all, usually as a few individuals in any given locality, and their presence can not be counted on, as in the usual case of fresh-water mollusks, and is distinctly a rarity in the temperate regions of the continent, where there are no well-defined wet and dry seasons.

## NOTES AND LITERATURE

### MIMICRY

IN some ways it would be a pity if the theory that mimicry has arisen through the operation of natural selection must be discarded since it is so ingenious in itself and was originated and fostered by such masters of theoretical biology. However, the old order seems to be surely giving place to new, here, as in other phases of the study of evolution. Since Wallace's "Papilionidæ of the Malayan Region" the case of *Papilio polytes* has been a classic. The females of this butterfly are of three sorts: one like the male *polytes*, one like *P. aristolochiæ* and the third like *P. hector*. The two latter species are supposed to be distasteful to insectivorous animals while *P. polytes* is supposed to be edible. The two "models" are numerous in individuals and while "*P. hector* and the *hector* form of *P. polytes* are confined to India and Ceylon, both *P. aristolochiæ* and the *aristolochiæ* form of *P. polytes* have a wider range eastward." The case is complete and has been convincing.

However, Punnett<sup>1</sup> found that in Ceylon

The following statements may be taken as a fair presentation of the facts:

1. In the low-country the male form of *polytes* female is at least as numerous as either of the other forms, and may be the most abundant of the three.

2. In the northeast of the island, in the *hector* country, the *aristolochiæ* form *polytes* is nearly as abundant as the *hector* form, though its model is at any rate exceedingly scarce.

3. Higher up-country, where *P. hector* is rare or absent and *P. aristolochiæ* is common, the *hector* form of *polytes* is more abundant than the *aristolochiæ* form.

It is obvious that these statements are not in harmony with the ideas of those who look to the theory of mimicry for an explanation of the polymorphism that exists among the females of *P. polytes*.

His observations concerning the enemies of butterflies confirm those of other heterodox students, namely: that "as serious enemies of butterflies in the imago state birds may be left out of

<sup>1</sup>"Mimicry in Ceylon Butterflies, with a Suggestion as to the Nature of Polymorphism," *Spolia Zeylanica*, Vol. VII, Part XXV, September, 1910.

account," that lizards "certainly do not appear to exercise that nice discrimination with regard to butterflies which is necessary for the establishment of mimicking forms on the theory of natural selection," and that asilids are not averse to preying upon "distasteful species."

After pointing out that the resemblances on which the theory was based are far less striking in living, moving specimens than in their expanded museum state, he says

Apart then from the questions whether the resemblances in many cases of mimicry are sufficiently close to be of effective service to the mimic, and whether the action of natural selection can be regarded as sufficiently stringent to have brought these resemblances into being, there are still the following difficulties in the way of the acceptance of the hypothesis of those who look to natural selection as an explanation of polymorphic forms in Lepidoptera:

1. The attribution of selection value to minute variation.
2. The absence of transitional forms.
3. The frequent absence of mimicry in the male sex.
4. The inability to offer an explanation of polymorphism, where the polymorphic forms can not be regarded as mimics of a distasteful species.

Moreover, the hypothesis assumes that minute variations of all sorts can be inherited, a position which at present is lacking in experimental proof.

The gist of the constructive part of his paper is as follows:

Natural selection plays no part in the *formation* of these polymorphic forms, but they are regarded as having arisen by sudden mutation, and series of transitional forms do not exist because such series are not biologically possible. Polymorphic forms may arise and may persist, provided that they are not harmful to the species, and it is possible to look upon their existence as due to the absence of natural selection rather than to the operation of this factor. . . . That polymorphism in a species should so frequently be confined to the female sex has long been remarked upon by those who study these matters, and the explanation most favored is that the female, burdened as she is with the next generation, is more exposed to the action of natural selection and in greater need of some protective adaptation. The weak point of such a view is that it does not explain why the male is not similarly protected. In connection with this problem recent Mendelian research on sex-limited inheritance is highly suggestive. It has been shown that certain types of inheritance receive their simplest explanation on the assumption that the female is heterozygous for a sex factor not contained in the male and that this sex factor may, on segregation of the gametes, repel the factor for some other character for which the female is also

heterozygous. From the beautiful experiments of Doncaster and Raynor it has been inferred that inheritance of this type occurs in the common currant moth (*Abraxis grossulariata*), where a distinct color variety, var. *lacticolor*, occurs. The factor for *grossulariata* pattern appears to segregate against the female sex factor, with the consequence that in only one type of mating, and that a rare one, is the *lacticolor* pattern transmitted to the male sex.

Gametic formulæ are suggested and the conditions they impose are mentioned, but no breeding work was done. Whether the above explanation of the behavior of *grossulariata* is correct or not and also the correctness of the suggested formulæ for *polytes* are immaterial to the present discussion. It is now well known that "mutations" do occur in the females of insects and that the new characters can be transferred to the male by proper breeding. But, why do the mutants of *P. polytes* resemble greatly, even if they do not do so to such an extent as had been supposed, other species? On account of similar anatomical and physiological make up; or, in this case, did the proper gametic couplings once take place so that the then new female type was transferred to the males (as in *grossulariata*) and was thereafter continued with such other modifications as were necessary to separate them taxonomically? In other words, the mimicking species came first and gave rise to the model!

Mutation, in itself, is not the whole story. Granting it, we must be given a reason for the mutant resembling something else and while the amendment just made to Punnett's paper *may* carry for this case, the chances are against it and we can not apply it to resemblances between species of different orders. In this connection, however, there seems to be an important thing which is often overlooked. It would be far more wonderful if, among the thousands of new forms which have arisen, there were no resemblances than it is that some of the forms are very much alike.

As Punnett and others have pointed out, the same process which brought about such a close resemblance between, for example, earwigs (Orthoptera) and rove beetles (Coleoptera) that they are frequently mixed in entomological collections doubtless caused also the resemblances (here called mimicry because an advantage can be imagined) between certain flies and certain stinging Hymenoptera. If "chance" or "environment" is used in the former case it is not unlikely that it applies in the latter also.

FRANK E. LUTZ.



